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COMPARATIVE CONFORMATION, ANATOMY, AND UDDER CHARACTERISTICS OF COWS OF CERTAIN BEEF AND DAIRY BREEDS[1]

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INTRODUCTION

The amount of secretory tissue in the udder has been shown by experiment to be very much less in a highly specialized beef cow than in a highly specialized dairy cow, even though the internal anatomy and the skeletal structure of the two cows are surprisingly similar (*8*).[3] These results suggested the possibility that the difference in amount of secretory tissue in the udder, together with differences in persistency of lactation, may constitute the chief hereditary characteristics responsible for the wide difference in milk-producing capacity which has long been known to exist between cows of the dairy and beef breeds.

Data on the quantity of secretory tissue in the udder were available for a large number of dairy cows whose milk-producing capacity and persistency of lactation had been determined. Similar data on the amount of secretory tissue in the udder of a beef cow, however, were limited to the individual used in the comparison mentioned (*8*). It seemed desirable, therefore, to determine whether or not the udder of the beef cow studied was typical of the udders of cows of the specialized beef breeds, and also to measure the producing capacity and the persistency or length of lactation of such beef cows when kept through their first lactation period under the same conditions of feeding, milking, and general management as dairy cows.

In order to make such a study possible a cooperative arrangement was made with the Animal Husbandry Division, Bureau of Animal Industry, in 1927, whereby that Division was to provide at the Iberia Livestock Experiment Farm, Jeanerette, La., a group of eight bred heifers of one of the beef breeds, suitable for such a study. In order to avoid as far as possible the influence of any inheritance of dairy-breed characters on milk-producing capacity, persistency of lactation, and mammary development, it appeared desirable to use beef animals that were registered or from registered parents, and that were of similar breeding. Animals of uniform size and condition, about 2 years of age and bred to calve within about 3 or 4 months, seemed most suitable for this study.

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[3] Reference is made by number (italic) to Literature Cited, p. 286.

The Bureau of Dairy Industry, for its part, agreed (1) to keep four of the animals through one lactation period under conditions of feeding, milking, and management comparable to those under which dairy animals of similar age and stage of lactation are kept at that station; (2) to keep the records of their production; (3) to obtain ante-mortem photographs and body measurements; (4) to obtain post-mortem anatomical data at the time of slaughter; and (5) to make a comparative study of the ante-mortem characteristics, the size, the capacity, and the gross anatomy and histology of their udders, according to the method regularly employed in studying the udders of dairy animals. These four animals were to be placed in the dairy barn at least 2 months before freshening, confined in stanchions, and fed and handled regularly to accustom them to the conditions of dairy-herd management before freshening, in order to avoid any rapid and permanent decline in milk flow which might result from a radical change in management at the very beginning of lactation. During the preliminary period in the dairy barn they were to be fed liberally to produce good development and conditioning without excessive fattening. Each animal was to be weighed every 28 days throughout the entire period of the experiment. After freshening, each cow in this group was to be milked twice daily; the quantity of milk produced at each milking was to be recorded, and a 2-day butterfat test was to be made each month. The ration was to be adjusted every 14 days and every effort was to be made to maintain lactation on a maximum plane and to continue it as long as possible. Breeding was to take place not earlier than 3 months and not later than 5 months after calving in order that the effect of gestation might not be a disturbing factor in comparing the quantity of milk produced or the persistency of lactation of cows of the beef and dairy breeds when kept under comparable conditions of dairy-herd management.

The other four animals, of similar breeding, size, age, condition, and gestation, were to be placed in the beef herd on the same experimental farm, and kept under conditions of management prevailing in that herd to show whether or not the difference in feeding and the regularity of milking beef cows kept under dairy-herd conditions would appreciably affect the size, capacity, abundance of secretory tissue, and gross and microscopic anatomy of their udders. On freshening, these animals would be permitted to run with their calves and would be fed the same as other cows in the beef herd. No attempt was to be made to measure milk- and butterfat-producing capacity or persistency of lactation, or to prolong the lactation period. Breeding was to take place according to the schedule usually followed in the beef herd. The only records to be kept on this group were those concerning breeding, calving, and live weight. After each animal had completed her lactation period, the conformation, anatomy, and comparative udder data were to be obtained according to the plan outlined for the group kept under dairy-herd conditions.

ANIMALS USED AND PROCEDURE FOLLOWED

In October 1927 three Hereford heifers (H–15, H–16, and H–17) from registered parents, all by the same sire and born in January 1926, were purchased from a Louisiana breeder. A search for additional animals suitable to make up the two groups was not immediately successful. Meanwhile the three animals were delivered at

the experimental farm and placed in the dairy barn. H–15 died from the effects of conditions induced by abnormal presentation of the fetus, and does not furnish any of the data on which this study is based.

The 2-day average weights of H–16 and H–17, as taken on October 27 and 28, 1927, were 720 and 695 pounds, respectively. On October 27 their ages were 21 months 22 days and 20 months 29 days. So far as the investigators know, normal weights for growing Hereford heifers have not been published. The average weight of these two animals, based on the 2-day average taken at the ages indicated, was 708 pounds. The herd in which H–16 and H–17 were raised received more individual attention than most herds in the vicinity, and the heifers purchased for the experiment were unusually tame and easily handled. They soon became accustomed to their new surroundings and conditions of management. They increased in weight and their general condition and behavior were satisfactory.

The three animals in this first lot were supposed to have been pasture-bred and pregnant when purchased. Breeding dates were not available except that none of the animals had been observed in heat since July 1927. However, on December 14, 1927, H–17 came in heat and was bred. H–16 was pregnant when purchased and calved normally on June 26, 1928. The loss of H–15 through death and the rebreeding of H–17 left only one of the animals originally purchased in suitable condition for use in the milking phase of the experiment. Consequently six additional Hereford heifers, 2 years of age and from registered parents, were selected in southern Texas. They were pasture-bred.

These heifers had been "roughing it" on pasture during the winter. They were shipped to Jeanerette, La., and during the first few days after their arrival they were kept tied, their horns were tipped, and they were branded. When examined, photographed, weighed, and measured on April 7, 1928, about a week after their arrival, they were thin and gaunt. They were below the average in size and condition for a breeder's herd, but were classed as good range cattle for the Gulf Coast region. Identification numbers were assigned to these heifers as follows: H–1, H–2, H–3, H–4, H–5, and H–6. Their weights on April 7 were, respectively, 550, 600, 580, 580, 625, and 595 pounds. Eighteen days later, on April 25, their weights were, respectively, 615, 660, 640, 645, 650, and 695 pounds. The minimum gain during that brief period was 25 pounds, the maximum 100 pounds, and the average 62.5 pounds. The weights of H–16 and H–17, on April 9, were 980 and 930 pounds. They had gained 260 and 235 pounds, respectively, since their arrival at the experiment station farm.

On June 4, 1928, the six heifers purchased in Texas were divided into two groups of three each on the basis of the uniformity of stage of gestation as determined by rectal examination. This basis for selection was used in order that those to be milked in the dairy barn might all freshen at about the same time and be in milk during the same period, thereby insuring more comparable conditions and facilitating the work required in carrying on the experiment. The pregnancy examination indicated that H–2, H–5, and H–6 were most nearly uniform and most advanced in stage of gestation, and they were selected for the group to be kept under dairy-herd conditions. Because of lack of uniformity in gestation, H–1, H–3, and H–4 were placed in the group to be kept under beef-herd conditions. In addition to the six heifers

purchased in Texas, two of the three animals originally purchased in Louisiana were still available, and in properly balancing the two groups it seemed desirable to place one of these older heifers in each group. H–16 was pregnant and apparently due to freshen within a month. H–17, though pregnant from a breeding on December 14, 1927, had reacted later to the agglutination test for infectious abortion. Since H–16 was more advanced in gestation and negative to the abortion test, she was placed in the group to be milked in the dairy barn, and H–17 was placed in the group to be kept under beef-herd conditions.

The group of Herefords consisting of H–2, H–5, H–6, and H–16, selected to be placed in the dairy herd, milked, and kept under conditions of dairy-herd management will subsequently be referred to as group 1. The group consisting of H–1, H–3, H–4, and H–17, selected to be kept in the beef herd under conditions of beef-herd management will be referred to as group 2.

Similar data for the Aberdeen Angus cow A–300 (*8*) and for two registered Holstein-Friesian cows (no. 299 and no. 827) were used for comparison with those obtained on the Herefords.

Figures 1, 2, and 3 show the animals used in this study.

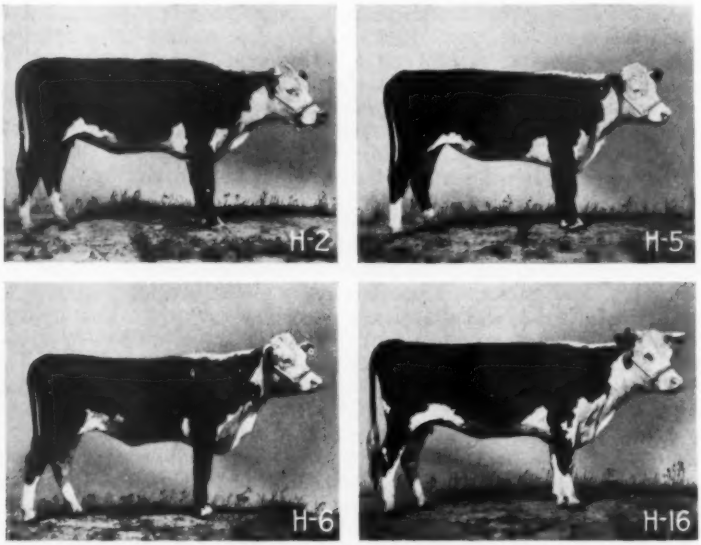

FIGURE 1.—The four Herefords (H–2, H–5, H–6, and H–16) that were kept in the dairy herd and milked through one lactation period.

THE HEREFORD EXPERIMENT

The details of the Hereford experiment were carried on essentially as outlined. The heifers in group 1 (dairy management) adjusted themselves slowly to the conditions prevailing in the dairy herd. Though not so gentle as animals raised under dairy conditions, they caused comparatively little trouble with the exception of occasional kicking. All of them calved normally. The heifers in group 2 (beef management) did not follow the schedule so well. The calving and breeding records of each of the animals in both groups are given in table 1.

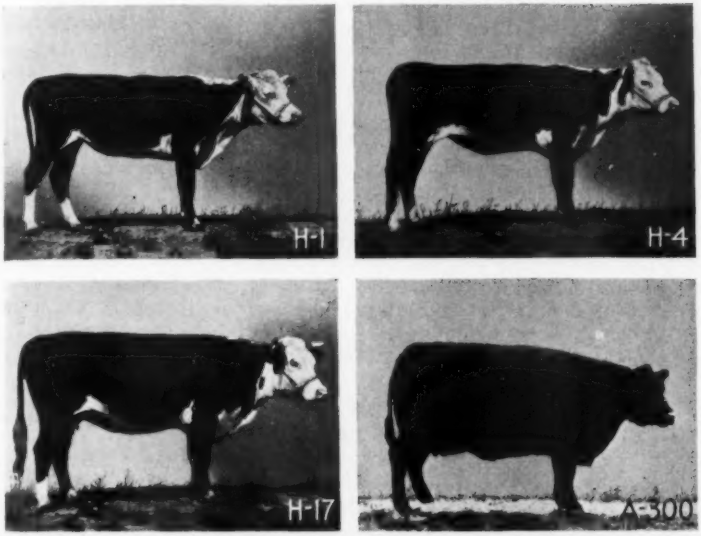

FIGURE 2.—The three Herefords (H-1, H-4, and H-17) that were kept in the beef herd; and the Aberdeen Angus cow (A-300) used for comparison.

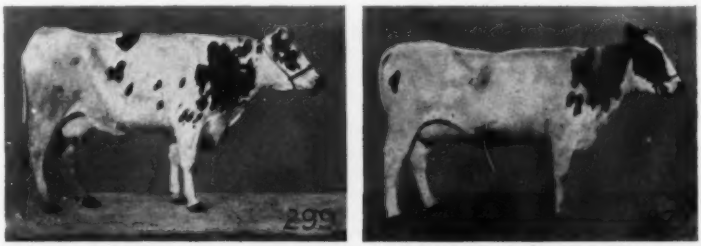

FIGURE 3.—The two Holstein-Friesian cows (no. 299 and no. 827) with which the Herefords and the Aberdeen Angus cow were compared.

TABLE 1.—*Calving and breeding records of Hereford heifers*

Group, and animal no.	Date of calving	Calving notes	Date rebred	Bred to—
Group 1 (dairy management):				
H-2	Oct. 1, 1928	Bull calf	Jan. 12, 1929	Hereford.
H-5	Oct. 17, 1928	Heifer calf	Apr. 9, 1929	Jersey.
H-6	Sept. 22, 1928	do	Mar. 21, 1929	Do.
H-16	June 26, 1928	do	Nov. 9, 1928	Hereford.
Group 2 (beef management):				
H-1	Dec. 14, 1928	Bull calf	(1)	
H-3 [2]				
H-4	Dec. 20, 1928	Aborted	(3)	Shorthorn.
H-17	June 12, 1928	do	Sept. 19, 1928	Brahman.

[1] Not bred. Nursed calf until late in May 1929.
[2] Died July 19, 1928. Disease diagnosed as anaplasmosis.
[3] Pasture-bred, after Mar. 1, 1929.

BODY WEIGHTS AND FEED CONSUMPTION

Every animal in group 1 was substantially heavier at the time of her final weight at the station on May 29, 30, and 31, 1929, than at the beginning of the experiment. Similar gains were made by the

animals in group 2 with the exception of H–1, which nursed her calf until a short time before the termination of the experiment. Each of the four animals in group 1 increased in weight during lactation, but remained nearly constant in weight after the completion of lactation. Two of the animals in group 2 made gains of approximately 100 pounds after calving, but H–1 showed a slight loss. The calf born to H–1 weighed 35 pounds at birth as compared with an average birth weight of 51 pounds for the calves born to the cows in group 1. All the calves were kept until they were at least 4 months old, when H–1's calf weighed 100 pounds as compared with an average of 160 pounds for the other four. So far as is known H–1's calf received nothing but its mother's milk and what feed it might have obtained while running with the herd. The other four calves were given whole milk for 30 days, and then skim milk. Grain and hay were first given at 1 week of age, the quantity being increased until the calves were consuming 3 pounds of grain and 3 to 4 pounds of hay daily at 3 months of age. The individual live weights for both groups of cows are given in table 2.

TABLE 2.—*Live weights of Herefords* [1]

Date	Group 1 (dairy management) [2]				Date	Group 2 (beef management) [3]		
	H–2	H–5	H–6	H–16		H–1	H–4	H–17
	Pounds	*Pounds*	*Pounds*	*Pounds*		*Pounds*	*Pounds*	*Pounds*
Oct. 27 and 28, 1927				720	Oct. 27 and 28, 1927			695
Nov. 9				770	Nov. 9			750
Dec. 7				790	Dec. 7			780
Jan. 4, 1928				820	Jan. 4, 1928			810
Feb. 1				890	Feb. 1			860
Feb. 29				910	Feb. 29			880
Mar. 28				880	Mar. 28			890
Apr. 7 or 9	600	625	595	980	Apr. 7 or 9	550	580	930
Apr. 25	660	650	695	930	Apr. 25	615	645	950
May 23	625	590	650	960	May 23	565	602	980
June 20	715	685	730	970	June 6	620	630	990
July 18	755	715	773	915	July 4	625	700	1,000
Aug. 16	745	710	772	902	Aug. 1	660	735	990
Sept. 12	780	735	805	922	Aug. 29	690	730	980
Oct. 10	695	720	680	913	Sept. 26	710	740	1,010
Nov. 7	745	665	725	942	Oct. 24	705	745	1,000
Dec. 5	720	700	760	950	Nov. 21	760	780	1,020
Jan. 2, 1929	760	710	790	970	Dec. 19	650	710	995
Jan. 30	750	705	760	955	Jan. 16, 1929	660	710	995
Feb. 27	790	735	790	995	Feb. 13	640	670	1,000
Mar. 27	760	690	730	940	Mar. 13	570	690	970
Apr. 24	790	730	780	960	Apr. 10	610	785	1,050
May 22	840	760	810	950	May 8	650	820	1,050
May 29, 30, and 31 [4]	835	775	792	953	May 29, 30, and 31 [4]	615	833	1,100
June 13 [5]	815	760	810	965	June 13 [5]	595	840	1,115
June 15 [5]	780	770	780	955	June 15 [5]	590	825	1,080

[1] H–15 and H–3 died during the early part of the experiment, consequently their weights are omitted.
[2] The heavy cross rules indicate the beginning and the end of the lactation period.
[3] The heavy cross rules indicate the beginning of the lactation period. The termination of the period is not definitely known. [4] At Jeanerette, La. [5] At Benning, D. C.

The four animals in group 1 were fed according to their calculated requirements (Savage standard plus 10 percent).

Table 3 shows the amounts of the various feeds consumed during the experiment. The hay was lespedeza, the silage was sorghum and soybean a part of the time and corn and soybean the remainder of the time. The grain mixture consisted of the following feeds: Brewers' rice, cottonseed meal, wheat bran, rice bran, rice polish, corn-and-cob meal, bone meal, and salt.

The cows were on pasture from June 21 to November 30, 1928, and from March 14 to May 29, 1929. From March 14 to 27, 1929, they were on pasture only half of each day.

The ration was the same as that fed the station's dairy herd during the same period.

TABLE 3.—*Feed consumed by Herefords in group 1 (dairy management) by 28-day periods (1928–29)*

Feeding period	H-2				H-5				H-6				H-16			
	Grain	Hay	Silage	Pasture	Grain	Hay	Silage	Pasture	Grain	Hay	Silage	Pasture	Grain	Hay	Silage	Pasture
	Lb.	*Lb.*	*Lb.*	*Dys.*	*Lb.*	*Lb.*	*Lb.*	*Dys.*	*Lb.*	*Lb.*	*Lb.*	*Dys.*	*Lb.*	*Lb.*	*Lb.*	*Dys.*
June 21 to July 18	----	----	----	28	----	----	----	28	----	----	----	28	84	----	----	28
July 19 to Aug. 15	----	----	----	28	----	----	----	28	----	----	----	28	91	----	----	28
Aug. 16 to Sept. 12	----	----	----	28	----	----	----	28	----	----	----	28	84	----	----	28
Sept. 13 to Oct. 10	42	----	----	28	----	----	----	28	35	----	----	28	70	----	----	28
Oct. 11 to Nov. 7	28	----	----	28	28	----	----	28	28	----	----	28	56	----	----	28
Nov. 8 to Dec. 5	28	84	420	23	28	84	420	23	28	84	420	23	56	84	420	23
Dec. 6 to Jan. 2	28	112	805	----	28	112	805	----	28	112	805	----	56	112	805	----
Jan. 3 to Jan. 30	28	140	840	----	28	140	840	----	28	140	840	----	49	140	840	----
Jan. 31 to Feb. 27	28	168	840	----	28	168	840	----	28	168	840	----	42	168	840	----
Feb. 28 to Mar. 27	28	140	330	7	28	140	330	7	28	140	330	7	42	140	330	7
Mar. 28 to Apr. 24	----	----	----	28	----	----	----	28	----	----	----	28	----	----	----	28
Apr. 25 to May 22	----	----	----	28	----	----	----	28	----	----	----	28	----	----	----	28
May 23 to June 19	----	----	----	7	----	----	----	7	----	----	----	7	----	----	----	7

RECORDS OF MILK PRODUCTION

The milk-producing capacity of the animals in group 1 was surprisingly low. Except for one animal, the duration of the lactation period was very brief, although the animals were milked until the quantity of milk obtained at a milking was extremely small, in an effort to continue lactation as long as possible. Furthermore, since no animal was bred until 102 days after calving, and one did not conceive until 180 days after calving, pregnancy could not have been responsible for the rapid decline in milk flow and the brevity of the lactation periods. Feeding a ration calculated to furnish an excess of nutrients was continued until the cows were turned on pasture March 14, 1929, at which time two of the animals (H–2 and H–6) were dry and the other two (H–5 and H–16) were producing respectively 0.8 pound and 3.5 pounds of milk daily. The records of milk and butterfat production are given in table 4.

The data presented in table 4 require but little discussion. The lack of persistency in the case of H–2, H–5, and H–6 is shown by the brevity of the periods of lactation, which were only 153 days, 202 days, and 159 days respectively. Moreover, the monthly production records, the averages for daily production, the averages for the first 10 days of lactation, the maxima for one milking and the maxima for 1 day, all bespeak the extremely low level of production for these three cows. Undoubtedly H–6 was the poorest milk and butterfat producer in the entire group, her total being only 80.6 pounds of milk and 3.73 pounds of butterfat for the entire lactation of 159 days—an average of only 0.51 pound of milk daily. Presumably H–16 was the oldest cow in the group. At any rate she was larger and better developed than any of the others. Though her milk flow was very low from a dairy standpoint it was more abundant and more persistent than that of any other cow in the group, her lactation period continuing for 329

days and her total production amounting to 1,767.8 pounds of milk and 90.52 pounds of butterfat. This is more than 11 times as much milk and 13 times as much butterfat as the average for the other three cows in the group. The fact that H–16 was so superior to the other animals in group 1 may be accounted for partly by her greater size and presumably more advanced age. Since she came from a different line of breeding, her inheritance may have been partly responsible for her higher production.

To confirm the statement previously made to the effect that the lactation period of these animals was prolonged to the extreme, attention is called to the fact that the average daily production for the last 10 days in milk was 0.20 pound for H–2, 0.50 pound for H–5, 0.17 pound for H–6, and 0.94 pound for H–16. On the last 2 days of lactation H–2 and H–6 were milked only once daily.

TABLE 4.—*Milk and butterfat production of Herefords in group 1 (dairy management)*

Year and month	H-2 [1]			H-5 [2]			H-6 [3]			H-16 [4]		
	Milk	Butterfat	Days milked	Milk	Butterfat	Days milked	Milk	Butterfat	Days milked	Milk	Butterfat	Days milked
1928:	*Lb.*	*Lb.*	*No.*	*Lb.*	*Lb.*	*No.*	*Lb.*	*Lb.*	*No.*	*Lb.*	*Lb.*	*No.*
June										8.8	.40	2
July										272.2	12.39	31
August										255.7	10.48	31
September							6.1	.31	3	226.8	10.21	30
October	52.1	3.05	28	34.7	1.41	10	30.1	1.51	31	184.5	10.79	31
November	31.0	1.57	30	57.3	2.32	30	18.3	.93	30	158.4	8.08	30
December	19.1	.86	31	43.9	1.49	31	10.2	.33	31	160.6	7.36	31
1929:												
January	14.2	.74	31	38.6	1.68	31	8.3	.39	31	139.5	7.74	31
February	8.6	.27	28	31.2	1.03	28	6.8	.23	28	114.8	7.00	28
March	1.0	.03	5	23.6	.78	31	.8	.03	5	117.1	7.08	31
April				20.5	.90	30				96.1	6.73	30
May				5.6	.25	11				33.3	2.26	23
Total	[5] 126.0	6.52	153	[6] 255.4	9.86	202	[7] 80.6	3.73	159	[8] 1,767.8	90.52	329
Daily average production:												
Entire period	.82			1.26			.51			5.37		
First 10 days	1.95			3.47			1.34			7.32		
Last 10 days	.20			.50			.17			.94		
Maximum production:												
For 1 milking	1.5			2.3			1.4			5.2		
For 1 day	2.6			4.1			2.4			10.1		

[1] Calved Oct. 1, 1928.
[2] Calved Oct. 17, 1928.
[3] Calved Sept. 22, 1928.
[4] Calved June 26, 1928.
[5] Butterfat test, 5.17 percent.
[6] Butterfat test, 3.86 percent.
[7] Butterfat test, 4.63 percent.
[8] Butterfat test, 5.12 percent.

During the time the Herefords were on experiment (June 26, 1928, to May 23, 1929) eight first-lactation Jerseys in the same herd were being tested for milk and butterfat production. Three of the Jerseys were in milk following abortions, whereas all of the Herefords in the group calved normally. Moreover, two and probably three of the Jerseys had had cattle-tick fever prior to going on test, contracted as a result of moving the herd from the experimental farm because of the flood. On the other hand, the Jerseys were slightly older when they freshened (average 3 years 1 month) and were milked three times daily during at least a part of the lactation period. The average production of the eight Jerseys was 6,684 pounds of milk and 358

pounds of butterfat. This is approximately 12 times the average milk production and approximately 13 times the average butterfat production of the four Herefords.

It is recognized that the Hereford is a specialized beef breed that has been bred for meat rather than dairy purposes. The Hereford cow consequently is expected to be a low milk producer, yet she seldom fails to raise a calf successfully without the aid of nurse cows—even under range conditions.

When compared with cows of a dairy breed of similar age, the production records of the four Herefords were extremely low. The animals in this group apparently did not possess the capacity to produce liberal quantities of milk, or the stimulus to continue lactation over an extended period. The fact that three of these animals were undersized is recognized, but with the opportunities afforded them both before and during lactation, they could hardly have failed to make a more creditable showing if their inheritance had included the capacity for abundant lactation.

BREED COMPARISONS

Since this study of the conformation, anatomy, udder characteristics, and lactating capacity of Herefords was prompted by results obtained in comparing the udder development of the Aberdeen Angus cow A–300 with that of the Jersey cow Sophie 19th of Hood Farm (*8*), it seemed fitting that an attempt be made to determine whether the conditions found in the udder of the Aberdeen Angus cow were typical of beef cows, and to what extent the Aberdeen Angus udder and the Hereford udders differ from the udders of cows of a dairy breed.

An effort was made to use for comparison the data from dairy cows of approximately the same age as the Herefords, but the only complete and comparable data available were those on two Holsteins that averaged 4 years 7 months of age at time of slaughter as compared with 3 to 3½ years for the Herefords. Moreover, the Aberdeen Angus cow was approximately 12 years of age when slaughtered. Attention is called to this difference in ages as it seems reasonable to suppose it might in some degree affect the size of the animals in the different groups and consequently be reflected in the direct weights and measurements of the body and its parts, and in the comparisons made in them. However, most of the data presented are in the form of ratios of one body measurement to another designed to show body proportions rather than absolute measurements, or are presented as ratios of the size of individual body parts to the body as a whole. A comparison of the data presented in this manner affords an opportunity to study conformation and comparative anatomy more or less irrespective of the size of the animals, and presumably minimizes to a great extent the effect of differences in age.

The Herefords, the Holsteins, and an Aberdeen Angus are compared on the basis of their conformation (ante-mortem data) and their anatomy (post-mortem data); and on the basis of the characteristics of their udders as determined both before and after death. The Aberdeen Angus cow was a show animal (had recently been exhibited at the International Livestock Exposition) and was in a very high condition of flesh, whereas the five Herefords purchased in southern Texas were in comparatively poor flesh. The Holsteins were in moderate flesh.

Holstein cow no. 299 was 4 years 2 months of age and had been dry 22 days when slaughtered. Her production record, made at the age of 3 years 3 months was 14,295 pounds of milk and 463 pounds of butterfat. Holstein cow no. 827 was 4 years 11 months of age, and had been dry 7 months 12 days when slaughtered. Her production record, made at 2 years 7 months of age, was 14,257 pounds of milk and 522 pounds of butterfat. Both Holsteins were milked three times daily while their records were being made. Milking the Holsteins three times instead of twice daily, and the fact that they were slightly more advanced in age at the time the records were made, probably gave them some advantage over the Herefords with respect to abundance of production. However, the difference between the production records of the Herefords and the Holsteins is so great that a marked contrast in producing capacity is emphatically shown. Production records are not available for the Aberdeen Angus cow A–300.

ANTE-MORTEM MEASUREMENTS AND SUPPLEMENTAL DATA

Owing to the lack of facilities at the Iberia Livestock Experiment Farm for slaughtering the Herefords and obtaining the desired post-mortem data, they were weighed on 3 successive days, given the necessary dippings at the Federal dipping station, and shipped to the stockyards at Benning, D. C., where they arrived June 8, 1929, after being en route since June 1.

On June 13 their weights were obtained on the stockyard scales, and photographs were taken of the individual animals. The total weight of the seven animals was 5,900 pounds as compared to 5,903 pounds for the average for 3 days immediately before shipment. Four animals had gained slightly in weight; three had lost. The individual weights are given in table 2.

On June 14, the cows were graded for slaughter purposes as follows:

	Grade
Group 1:	
H–2	Low good.
H–5	Middle medium.
H–6	Low medium.
H–16	Middle good.
Group 2:	
H–1	Top cutter.
H–4	Top medium.
H–17	Low good.

On June 15, at the Benning stockyards, ante-mortem measurements, designed to translate conformation into numerical values suitable for analysis, were made of each of the seven animals according to the plan regularly followed by the Bureau of Dairy Industry in recording and studying growth and conformation. Observations on the development and condition of the udder of each of the seven cows were made on the same day. Live weights, taken at about 2 p. m. on June 15, totaled 5,780 pounds. Individual weights are shown in table 2.

A comparison of the conformation of animals representing such marked differences in type as animals of dairy and beef breeds is difficult to show, except as it can be shown through body proportions, or through the relation of each of the different measurements to one or more measurements selected as most nearly representing the skeletal size of the animal. Bush-Brown (*2*), a sculptor, Washington, D. C., emphasized the necessity for—

an accurate and reliable method of measuring the bodies of individuals, which will make full allowance for variations in size, so that not only large and small individuals of the same breed may become comparable, but also individuals belonging to different breeds, and even the same individual at different stages of growth.

Such a method must clearly be based upon a unit common to all individuals, and upon a comparison of proportions rather than upon absolute measurements. In studying the conformation of the horse, Bush-Brown used as a basis the height at withers which, regardless of the size of the animal, determines the unit of measure to be used for that animal. The proportions obtained from measurements made on this basis enable an artist or a sculptor to reproduce with exactness a painting or a model of any size.

A number of research workers who have studied cattle conformation have indicated that height at withers is a fairly satisfactory measure of skeletal size. According to the views of Van den Bosch, late chief inspector of the Netherlands Cattle Society, a dairy cow approaches perfection as her different body measurements approach definite proportions to height at withers. He uses height at withers as a basis for determining body proportions in evaluating the degree of perfection in the form of a dairy cow. Eckles and Swett (*3, p. 9*) state that—

> growth of the animal, as far as the skeleton is concerned can be determined reasonably well by a few measurements, and sufficiently well for most purposes by one measurement alone.

The one selected was height at withers. Brody (*1, p. 1*) states that—

> since height at withers in cattle is but slightly influenced by environmental conditions, therefore, at a given age the numerical value of this measurement is practically a genetic index of the size of the animal.

More recently Lush and Copeland (*6, p. 49*) stated:

> For most purposes a very few measurements considered in relation to each other or in relation to weight seem as much as would be really useful in contributing to the general picture of the animal and of the changes which occurred in it. Thus height over withers or over hips would certainly be included among those measurements least influenced by plane of nutrition, and therefore especially apt to be illuminating when considered in relation to weight.

Other workers, studying nutrition, growth, and other matters relating to size in cattle, have based their experiments either on skeletal size alone or on skeletal size and live weight—skeletal size being measured by height at withers.

Some students of animal conformation subscribe to the idea that length of head rather than height at withers is the fundamental unit of measurement to which every other body measurement bears a definite ratio in the animal having the desirable form. Pontius (*7, p. 110*) studied the relation between length of head and each of 10 different body measurements for a group of dairy cows having good conformation and good producing capacity. His correlations were not highly significant. According to Gulliver (*5, p. 69*), both Megargee and Kawamura, who are well known as animal painter and animal sculptor respectively, have for years used a system of measurement and proportion based on length of head.

The ante-mortem measurements of the seven Herefords, together with corresponding measurements of the two Holstein cows and the Aberdeen Angus cow, whose udders are compared with those of the Herefords later in this paper are given in table 5.

TABLE 5.—*Ante-mortem data on the animals used in the experiments*

Item	Herefords								Holsteins			Aberdeen Angus
	Group 1 (dairy management)				Group 2 (beef management)			Average	No. 299	No. 827	Average	A-300
	H-2	H-5	H-6	H-16	H-1	H-4	H-17					
Age	(1)	(1)	(1)	(1)	(1)	(1)	(1)		(2)	(2)		(4)
Condition of flesh.....grade	6	6	6	7	4	7	8		5	7		9
Time since calving.....mos-days	8-14	8-0	8-23	11-19			12-3		11-14	14-7		32-0
Thickness of hide:												
At thirteenth rib.....centimeters	1.04	0.97	1.34	1.11	1.01	1.18	0.88		1.00	1.04		1.32
At rear of udder.....do	0.63	0.52	0.62	0.60	0.56	0.65	0.55		0.45	0.71		0.56
Diameter of trachea.....do	5.39	5.10	4.97		4.34	5.14						
Live weight:												
Actual weight.....pounds	780	770	780	955	590	825	1,080	826	1,400	1,375	1,388	1,565
Ratio to height at withers	6.63	6.82	6.69	8.16	5.33	6.79	8.89	7.04	9.80	10.27	10.04	12.81
Ratio to length of head		17.40	18.25	20.21	13.72	18.44	22.38	18.40	26.17	25.46	25.82	33.48
Height at withers:												
Actual measurement.....centimeters	117.67	112.92	116.58	117.00	110.75	121.50	121.50	116.85	142.92	133.83	138.38	122.13
Ratio to height at withers	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Ratio to length of head		2.55	2.73	2.48	2.58	2.72	2.52	2.60	2.67	2.48	2.58	2.61
Height at hips:												
Actual measurement.....centimeters	118.92	116.08	115.58	117.33	112.75	119.50	124.58	117.82	145.33	135.00	140.17	121.71
Ratio to height at withers	1.01	1.03	0.99	1.00	1.02	0.98	1.03	1.01	1.02	1.01	1.02	1.00
Ratio to length of head		2.62	2.70	2.48	2.62	2.67	2.58	2.61	2.72	2.50	2.61	2.60
Height at pinbones:												
Actual measurement.....centimeters	114.33	112.50	112.25	113.88	108.75	116.75	116.58	113.58	132.83	131.83	132.33	119.25
Ratio to height at withers	0.97	1.00	0.96	0.97	0.98	0.96	0.96	0.97	0.93	0.99	0.96	0.98
Ratio to length of head		2.54	2.63	2.41	2.53	2.61	2.42	2.52	2.48	2.44	2.46	2.55
Height of back at first lumbar vertebra:												
Actual measurement.....centimeters	117.25	115.25	115.00	116.42	111.25	120.00	120.42	116.51	144.25	131.58	137.92	124.75
Ratio to height at withers	1.00	1.02	0.99	1.00	1.00	0.99	0.99	1.00	1.01	0.98	1.00	1.02
Ratio to length of head		2.60	2.69	2.46	2.59	2.68	2.50	2.59	2.70	2.44	2.57	2.67
Depth of fore chest:												
Actual measurement.....centimeters	63.38	62.88	62.88	65.13	58.25	63.13	64.75	62.91	77.25	74.00	75.63	75.00
Ratio to height at withers	0.54	0.56	0.54	0.56	0.53	0.52	0.53	0.54	0.54	0.55	0.55	0.61
Ratio to length of head		1.42	1.47	1.38	1.35	1.41	1.34	1.40	1.44	1.37	1.41	1.60
Depth of rear chest:												
Actual measurement.....centimeters	62.00	61.75	61.63	64.50	57.63	62.63	65.50	62.23	78.88	73.50	76.19	78.25
Ratio to height at withers	0.53	0.55	0.53	0.55	0.52	0.52	0.54	0.53	0.55	0.55	0.55	0.64
Ratio to length of head		1.40	1.44	1.37	1.34	1.40	1.36	1.39	1.47	1.36	1.42	1.67
Depth of paunch:												
Actual measurement.....centimeters	62.88	62.38	62.50	65.00	56.63	63.88	68.13	63.06	80.13	74.17	77.15	80.25
Ratio to height at withers	0.53	0.55	0.54	0.56	0.51	0.53	0.56	0.54	0.56	0.55	0.56	0.66
Ratio to length of head		1.41	1.46	1.38	1.32	1.43	1.41	1.40	1.50	1.37	1.44	1.72

Length, withers to hips (standard):												
Actual measurement centimeters	81.50	83.50	81.00	84.50	82.00	81.50	87.00	83.00	93.50	98.00	95.75	86.25
Ratio to height at withers	0.69	0.74	0.69	0.72	0.74	0.67	0.72	0.71	0.65	0.73	0.69	0.71
Ratio to length of head	----------	1.89	1.89	1.79	1.91	1.82	1.80	1.85	1.75	1.81	1.78	1.84
Length, hips to pinbones (standard):												
Actual measurement centimeters	40.50	39.50	41.00	44.25	37.50	39.75	44.00	40.93	48.50	47.50	48.00	45.88
Ratio to height at withers	0.34	0.35	0.35	0.38	0.34	0.33	0.36	0.35	0.34	0.35	0.35	0.38
Ratio to length of head	----------	0.89	0.96	0.94	0.87	0.89	0.91	0.91	0.91	0.88	0.90	0.98
Total length, withers to pinbones (standard):												
Actual measurement centimeters	122.00	123.00	122.00	128.75	119.50	121.25	131.00	123.93	142.00	145.50	143.75	132.13
Ratio to height at withers	1.04	1.09	1.05	1.10	1.08	1.00	1.08	1.06	0.99	1.09	1.04	1.08
Ratio to length of head	----------	2.78	2.85	2.72	2.78	2.71	2.72	2.76	2.65	2.69	2.67	2.83
Length of loin:												
Actual measurement centimeters	35.00	35.75	35.25	36.00	35.00	37.25	37.25	35.93	42.00	37.75	39.88	----------
Ratio to height at withers	0.30	0.32	0.30	0.31	0.32	0.31	0.31	0.31	0.29	0.28	0.29	----------
Ratio to length of head	----------	0.81	0.82	0.76	0.81	0.83	0.77	0.80	0.79	0.70	.075	----------
Length of rump:												
Actual measurement centimeters	35.00	34.00	35.00	39.00	33.00	35.00	37.00	35.43	42.00	39.00	40.50	41.50
Ratio to height at withers	0.30	0.30	0.30	0.33	0.30	0.29	0.30	0.30	0.29	0.29	0.29	0.34
Ratio to length of head	----------	0.77	0.82	0.83	0.77	0.78	0.77	0.79	0.79	0.72	0.76	0.89
Length, point of shoulder to pinbones:												
Actual measurement centimeters	142.13	139.00	140.75	148.13	139.63	144.25	148.88	143.25	161.00	166.63	163.82	----------
Ratio to height at withers	1.21	1.23	1.21	1.27	1.26	1.19	1.23	1.23	1.13	1.25	1.19	----------
Ratio to length of head	----------	3.14	3.29	3.14	3.25	3.22	3.09	3.19	3.01	3.09	3.05	----------
Length of head (caliper):												
Actual measurement centimeters	----------	44.25	42.75	47.25	43.00	44.75	48.25	[5] 45.04	53.50	54.00	53.75	46.75
Ratio to height at withers	----------	0.39	0.37	0.40	0.39	0.37	0.40	[5] 0.39	0.37	0.40	0.39	0.38
Ratio to length of head	----------	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Width of fore chest:												
Actual measurement centimeters	34.42	34.25	36.08	41.75	33.42	34.50	43.33	36.82	54.25	49.83	52.04	61.00
Ratio to height at withers	0.29	0.30	0.31	0.36	0.30	0.28	0.36	0.31	0.38	0.37	0.38	0.50
Ratio to length of head	----------	0.77	0.84	0.88	0.78	0.77	0.90	0.82	1.01	0.92	0.97	1.30
Width of rear chest:												
Actual measurement centimeters	48.25	47.92	48.00	55.25	45.42	49.92	61.00	50.82	62.94	64.50	63.72	65.75
Ratio to height at withers	0.41	0.42	0.41	0.47	0.41	0.41	0.50	0.43	.44	0.48	0.46	0.54
Ratio to length of head	----------	1.08	1.12	1.17	1.06	1.12	1.26	1.14	1.18	1.19	1.19	1.41
Width of paunch:												
Actual measurement centimeters	51.58	53.75	53.75	63.83	49.50	58.83	70.75	57.43	65.00	71.08	68.04	73.75
Ratio to height at withers	0.44	0.48	0.46	0.55	0.45	0.48	0.58	0.49	0.45	0.53	0.49	0.60
Ratio to length of head	----------	1.21	1.26	1.35	1.15	1.31	1.47	1.29	1.21	1.32	1.27	1.58
Width of hips:												
Actual measurement centimeters	48.00	46.25	47.25	50.00	45.00	47.50	52.50	48.07	55.75	55.75	55.75	65.50
Ratio to height at withers	0.41	0.41	0.41	0.43	0.41	0.39	0.43	0.41	0.39	0.42	0.41	0.54
Ratio to length of head	----------	1.05	1.11	1.06	1.05	1.06	1.09	1.07	1.04	1.03	1.04	1.40
Width of thurls:												
Actual measurement centimeters	41.00	41.75	46.00	45.50	39.50	43.50	45.00	43.18	54.00	50.75	52.38	52.38
Ratio to height at withers	0.35	0.37	0.39	0.39	0.36	0.36	0.37	0.37	0.38	0.38	0.38	0.43
Ratio to length of head	----------	0.94	1.08	0.96	0.92	0.97	0.93	0.97	1.01	0.94	0.98	1.12

[1] 3 to 3½ years. [2] 4 years 2 months. [3] 4 years 11 months. [4] About 12 years. [5] Based on 6 animals.

TABLE 5.—*Ante-mortem data on the animals used in the experiments*—Continued

Item	Herefords								Holsteins			Aberdeen Angus
	Group 1 (dairy management)				Group 2 (beef management)			Average	No. 299	No. 827	Average	A-300
	H-2	H-5	H-6	H-16	H-1	H-4	H-17					
Width of pinbones:												
Actual measurement.....centimeters	27.50	29.50	32.50	31.00	24.50	29.50	31.00	29.36	39.50	37.50	38.50	34.50
Ratio to height at withers	0.23	0.26	0.28	0.26	0.22	0.24	0.26	0.25	0.28	0.28	0.28	0.28
Ratio to length of head		0.67	0.76	0.66	0.57	0.66	0.64	0.66	0.74	0.69	0.72	0.74
Width of loin:												
Actual measurement.....centimeters	28.25	27.75	29.75	31.50	27.75	29.50	32.25	29.54	35.00	41.25	38.13	
Ratio to height at withers	0.24	0.25	0.26	0.27	0.25	0.24	0.27	0.25	0.24	0.31	0.28	
Ratio to length of head		0.63	0.70	0.67	0.65	0.66	0.67	0.66	0.65	0.76	0.71	
Width of forehead (caliper):												
Actual measurement.....centimeters		16.75	16.00	16.75	17.25	18.00	17.50	17.04	17.75	19.00	18.38	17.38
Ratio to height at withers		0.15	0.14	0.14	0.16	0.15	0.14	0.15	0.12	0.14	0.13	0.14
Ratio to length of head		0.38	0.37	0.35	0.40	0.40	0.36	0.38	0.33	0.35	0.34	0.37
Width across eyes:												
Actual measurement.....centimeters		20.00	20.25	21.50	20.00	20.75	21.50	20.67		23.25	[6] 23.25	
Ratio to height at withers		0.18	0.17	0.18	0.18	0.17	0.18	0.18		0.17	[6] 0.17	
Ratio to length of head		0.45	0.47	0.46	0.47	0.46	0.45	0.46		0.43	0.43	
Circumference of fore chest:												
Actual measurement.....centimeters	165.50	163.50	164.00	175.00	151.00	165.00	179.00	166.14	214.00	200.00	207.00	230.00
Ratio to height at withers	1.41	1.45	1.41	1.50	1.36	1.36	1.47	1.42	1.50	1.49	1.50	1.88
Ratio to length of head		3.69	3.84	3.70	3.51	3.69	3.71	3.69	4.00	3.70	3.85	4.92
Circumference of rear chest:												
Actual measurement.....centimeters	182.00	177.00	177.00	197.50	167.50	182.00	211.00	184.86	231.50	224.00	227.75	241.50
Ratio to height at withers	1.55	1.57	1.52	1.69	1.51	1.50	1.74	1.58	1.62	1.67	1.65	1.98
Ratio to length of head		4.00	4.14	4.18	3.90	4.07	4.37	4.11	4.33	4.15	4.24	5.17
Circumference of paunch:												
Actual measurement.....centimeters	189.00	191.00	190.00	209.00	173.00	198.00	226.50	196.64	236.00	238.00	237.00	261.00
Ratio to height at withers	1.61	1.69	1.63	1.79	1.56	1.63	1.86	1.68	1.65	1.78	1.72	2.14
Ratio to length of head		4.32	4.44	4.42	4.02	4.42	4.69	4.39	4.41	4.41	4.41	5.58
Circumference of muzzle:												
Actual measurement.....centimeters	52.00	46.00	45.00	48.00	45.00	44.50	47.50	46.86	52.00	54.00	53.00	47.75
Ratio to height at withers	0.44	0.41	0.39	0.41	0.41	0.37	0.39	0.40	0.36	0.40	0.38	0.39
Ratio to length of head		1.04	1.05	1.02	1.05	0.99	0.98	1.02	0.97	1.00	0.99	1.02
Circumference of shinbone:												
Actual measurement.....centimeters	17.00	17.75	17.50	18.00	16.50	17.75	17.75	17.46	18.75	19.25	19.00	18.75
Ratio to height at withers	0.14	0.16	0.15	0.15	0.15	0.15	0.15	0.15	0.13	0.14	0.14	0.15
Ratio to length of head		0.40	0.41	0.38	0.38	0.40	0.37	0.39	0.35	0.36	0.36	0.40

[6] Based on 1 animal.

BREED DIFFERENCES IN UNITS OF MEASUREMENT AND IN RATIOS TO HEIGHT AT WITHERS AND TO LENGTH OF HEAD

When expressed in actual units, the measurements of the Herefords differed considerably from each other, and as a group differed markedly from the Holsteins and from the Aberdeen Angus. Undoubtedly, condition of fleshing and stage of gestation had a considerable effect on the measurements of individual animals, as H–1 was in comparatively poor flesh, H–17 was in very good flesh and nearly due to freshen, and A–300 was in a very high condition of flesh.

The ratio of each body measurement to height at withers and to length of head, which, as stated, have been used by several investigators as basic measurements, have been determined to make possible a study of the comparative proportions of each animal. Table 5 shows the body measurements for the different items expressed in actual units, and the ratios of the body measurements to the height at withers and to the length of head. Thickness of hide and diameter of trachea are not considered as body measurements, consequently they are not included in the discussion of conformation.

Without exception the average for live weight, and for each body measurement, expressed in actual units, was greater for the Holsteins than for the Herefords, but the relation of actual measurements of the Aberdeen Angus to those of the other breeds is not consistent. The probable effect of age differences on these absolute measurements has been mentioned previously. Twenty-four different body measurements are compared for each of the breeds. The magnitude of the measurement for the Aberdeen Angus is intermediate between the averages for the Herefords and the Holsteins for 13 of these items, 8 of which are indicative of "scale." The width of thurls of the Aberdeen Angus is equal to the corresponding average for Holsteins but distinctly greater than the Hereford average. The measurements for the remaining 10 items, which include the depths of rear chest and of paunch; length of rump; width of hips; and the widths and circumferences of fore chest, rear chest, and paunch, are greater for the Aberdeen Angus than for either the Herefords or the Holsteins. Undoubtedly most of these 10 measurements, as well as the width of thurls, were affected to a very considerable extent by the excessive fleshing in the Aberdeen Angus.

PERCENTAGE DIFFERENCES, BY BREEDS, IN UNITS OF MEASUREMENT AND IN RATIOS

In comparing breed averages on the basis either of actual units of measurement or of ratios, some differences which at first appeared small were found to be of considerable importance if they represented small measurements or low ratios. Some differences that appeared relatively large were of comparatively little significance if they represented large measurements or high ratios. For example, in comparing the averages for Holsteins with those for Herefords (table 5), a difference of 21.53 centimeters in height at withers represents a percentage of 18.4, whereas a difference of only 8.59 centimeters in width of loin is equivalent to 29.1 percent. For this reason the differences in breed averages were reduced to a percentage basis. To determine the percentage to which the Holsteins differed from the Herefords for any given item the difference between the averages for the two breeds for that item was divided by the average for the

TABLE 6.—*Comparative conformation of the Herefords, Holsteins, and Aberdeen Angus*

Item	Actual units			Ratios based on heights at withers			Ratios based on length of head		
	Relation of Holsteins to Herefords	Relation of Aberdeen Angus to Herefords	Relation of Aberdeen Angus to Holsteins	Relation of Holsteins to Herefords	Relation of Aberdeen Angus to Herefords	Relation of Aberdeen Angus to Holsteins	Relation of Holsteins to Herefords	Relation of Aberdeen Angus to Herefords	Relation of Aberdeen Angus to Holsteins
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Live weight	+68.04	+89.47	+12.75	+42.61	+81.96	+27.59	+40.33	+81.96	+29.67
Height at withers	+18.43	+4.52	−11.74				−.77	+.38	+1.16
Height at hips	+18.97	+3.30	−13.17	+.99	−.99	−1.96	±.00	−.38	−.38
Height at pinbones	+16.51	+4.99	−9.88	−1.03	+1.03	+2.08	−2.38	+1.19	+3.66
Height of back at first lumbar vertebra	+18.38	+7.07	−9.55	±.00	+2.00	+2.00	−.77	+3.09	+3.89
Depth of fore chest	+20.22	+19.22	−.83	+1.85	+12.96	+10.91	+.71	+14.29	+13.48
Depth of rear chest	+22.43	+25.74	+2.70	+3.77	+20.75	+16.36	+2.16	+20.14	+17.61
Depth of paunch	+22.34	+27.26	+4.02	+3.70	+22.22	+17.86	+2.86	+22.86	+19.44
Length, withers to hips (standard)	+15.36	+3.92	−9.92	−2.82	±.00	+2.90	−3.78	−.54	+3.37
Length, hips to pinbones (standard)	+17.27	+12.09	−4.42	±.00	+8.57	+8.57	−1.10	+7.69	+8.89
Total length, withers to pinbones	+15.99	+6.62	−8.08	−1.89	+1.89	+3.85	−3.26	+2.54	+5.99
Length of loin	+10.99			−6.45			−6.25		
Length of rump	+14.31	+17.13	+2.47	−3.33	+13.33	+17.24	−3.80	+12.66	+17.11
Length, point of shoulder to pinbones	+14.36			−3.25			−4.39		
Length of head (caliper)	+19.34	+3.80	−13.02	±.00	−2.56	−2.56			
Width of fore chest	+41.34	+65.67	+17.22	+22.58	+61.29	+31.58	+18.29	+58.54	+34.02
Width of rear chest	+25.38	+29.38	+3.19	+6.98	+25.58	+17.39	+4.39	+23.68	+18.49
Width of paunch	+18.47	+28.42	+8.39	±.00	+22.45	+22.45	−1.55	+22.48	+24.41
Width of hips	+15.98	+36.26	+17.49	±.00	+31.71	+31.71	−2.80	+30.84	+34.62
Width of thurls	+21.31	+21.31	±.00	+2.70	+16.22	+13.16	+1.03	+15.46	+14.29
Width of pinbones	+31.13	+17.51	−10.39	+12.00	+12.00	±.00	+9.09	+12.12	+2.78
Width of loin	+29.08			+12.00			+7.58		
Width of forehead (caliper)	+7.86	+2.00	−5.44	−13.33	−6.67	+7.69	−10.53	−2.63	+8.82
Width across eyes	+12.48			−5.56			−6.52		
Circumference of fore chest	+24.59	+38.44	+11.11	+5.63	+32.39	+25.33	+4.34	+33.33	+27.79
Circumference of rear chest	+23.20	+30.64	+6.04	+4.43	+25.32	+20.00	+3.16	+25.79	+21.93
Circumference of paunch	+20.52	+32.73	+10.13	+2.38	+27.38	+24.42	+.46	+27.11	+26.53
Circumference of muzzle	+13.10	+1.90	−9.91	−5.00	−2.50	+2.63	−2.94	±.00	+3.03
Circumference of shinbone	+8.82	+7.39	−1.32	−6.67	±.00	+7.14	−7.69	+2.56	+11.11

Herefords and multiplied by 100. If the Holstein average was higher than the Hereford average, the percentage value was prefixed with a plus sign; if lower it was prefixed with a minus sign. In the same manner the data for the Aberdeen Angus were compared first with the Herefords and then with the Holsteins. The percentages showing the extent to which the breeds differ are given in table 6.

Since all the weights and measurements are greater for Holsteins than for Herefords, the percentages showing the degree of difference are all plus. The greatest difference, which is for live weight, shows that the Holsteins averaged 68.04 percent heavier than the Herefords. Among the measurements, the greatest difference was in width of fore chest (41.34 percent), and the next in width of pinbones (31.13 percent). The greatest differences appear to be associated with fullness of barrel and the smallest with skeletal measurements and "scale."

The Aberdeen Angus differs from the Herefords most in live weight, widths and circumferences, and least in skeletal measurements and "scale."

The Aberdeen Angus is higher than the Holsteins in weight, lower than the Holsteins for 13 of the measurements, higher for 10, and the same for 1. The measurements having the greatest minus difference are height at withers and hips, length of head, and width of pinbones. Those having the greatest plus difference are width of fore chest and hips and circumference of fore chest and paunch.

The ratios based on height at withers indicate that the Holsteins were very similar to the Herefords in body proportions with only a few of the items differing greatly, the larger differences being confined almost entirely to measurements of width. The Aberdeen Angus differed most from both the Herefords and the Holsteins in width of hips, depth of paunch, and in widths and circumferences of barrel, showing the combined effect on body proportions of a high condition of flesh in a low-set animal.

The comparison of the ratios based on length of head emphasizes the similarity in the proportions of the Herefords and Holsteins for nearly all items; it shows that the Aberdeen Angus differed only slightly from the Herefords and the Holsteins in the items representing "scale", but that the Aberdeen Angus differed greatly from both Herefords and Holsteins in many of the widths and in all of the circumferences of the barrel. In view of these results it is noteworthy that the Herefords and the Aberdeen Angus, though differing greatly in size and in many body measurements, were nearly the same in length of head, and that the Holsteins greatly exceeded them in this measurement.

Although marked differences existed in the live weight and in many of the body dimensions of the breeds, a similarity is shown in the body proportions of the Holsteins and the Herefords when the ante-mortem data are compared on the basis of ratios based either on height at withers or on length of head. Also the ratios for measurements of height and length, which are indicative of "scale", indicate that the three breeds are very similar. The outstanding differences in body proportions are for those measurements that are most affected by deposition of fat. This confirms conclusions previously expressed (*8*) that cows of the different breeds are generally similar in skeletal structure, and that difference in type resulting from breeding and selection is due primarily to degree of fleshing.

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TABLE 7.—*Supplemental ante-mortem data on the animals used in the experiments*

Item	Herefords								Holsteins			Aberdeen Angus
	Group 1 (dairy management)				Group 2 (beef management)			Average				
	H-2	H-5	H-6	H-16	H-1	H-4	H-17		No. 299	No. 827	Average	A-300
Contour area of fore chest:												
Total area—square centimeters	1,692	1,657	1,742	2,053	1,443	1,721	2,122	1,776	3,112	2,747	2,930	3,960
Portion above vertical midpoint—percent	52.6	53.3	51.3	51.1	53.6	52.2	50.5	52.1	48.6	49.6	49.1	51.1
Portion below vertical midpoint—do	47.4	46.7	48.7	48.9	46.4	47.8	49.5	47.9	51.4	50.4	50.9	48.9
Total area divided by depth of fore chest—ratio	26.7	26.4	27.7	31.5	24.8	27.3	32.8	28.2	40.3	37.1	38.7	52.8
Total area divided by width of fore chest—do	49.2	48.4	48.3	49.2	43.2	49.9	49.0	48.2	57.4	55.1	56.3	64.9
Total area divided by circumference of fore chest—ratio	10.2	10.1	10.6	11.7	9.6	10.4	11.9	10.6	14.5	13.7	14.1	17.2
Contour area of paunch:												
Total area—square centimeters	2,602	2,634	2,663	3,233	2,145	2,891	3,841	2,858	3,910	4,127	4,019	4,916
Portion above vertical midpoint—percent	49.0	49.1	48.9	47.9	48.9	48.1	48.3	48.6	44.8	49.6	47.2	49.3
Portion below vertical midpoint—do	51.0	50.9	51.1	52.1	51.1	52.0	51.7	51.4	55.3	50.4	52.9	50.8
Total area divided by depth of paunch—ratio	41.4	42.2	42.6	49.7	37.9	45.3	56.4	45.1	48.8	55.6	52.2	61.3
Total area divided by width of paunch—do	50.5	49.0	49.5	50.7	43.3	49.1	54.3	49.5	60.2	58.1	59.2	66.7
Total area divided by circumference of paunch—ratio	13.8	13.8	14.0	15.5	12.4	14.6	17.0	14.4	16.6	17.3	17.0	18.8
Body surface area—square centimeters	41,323	40,816	41,224	46,285	36,337	42,067	48,838	42,413	57,742	58,132	57,937	57,030
Volume of barrel—cubic centimeters	174,689	174,076	179,022	233,300	152,020	191,149	253,529	195,398	346,962	344,800	345,881	356,447
Angle of rump (clinometer)—degrees—minutes	−7°55′	−7°10′	−7°27′	−5°24′	−8°26′	−6°14′	−13°18′	−7°59′	−15°48′	−4°54′	−10°21′	−3°52′
Thoracic index	1.841	1.836	1.743	1.560	1.743	1.830	1.494	1.721	1.424	1.485	1.455	1.230
Abdominal index	1.219	1.161	1.163	1.018	1.144	1.086	0.963	1.108	1.233	1.043	1.138	1.088
Legginess	0.461	0.443	0.461	0.443	0.474	0.480	0.467	0.461	0.459	0.447	0.453	0.386
Wedge shape:												
Based on differences in measurements—												
Depth of paunch minus depth of fore chest—centimeters	−0.50	−0.50	−0.38	−0.13	−1.62	0.75	3.38	0.14	2.88	0.17	1.53	5.25
Width of paunch minus width of fore chest—centimeters	17.16	19.50	17.67	22.08	16.08	24.33	27.42	20.61	10.75	21.25	16.00	12.75
Circumference of paunch minus circumference of fore chest—centimeters	23.50	27.50	26.00	34.00	22.00	33.00	47.50	30.50	22.00	38.00	30.00	31.00
Contour area of paunch minus contour area of fore chest—square centimeters	910	977	921	1,180	703	1,170	1,719	1,083	798	1,380	1,089	956
Based on ratios of measurements—												
Depth of paunch divided by depth of fore chest—ratio	0.992	0.992	0.994	0.998	0.972	1.012	1.052	1.002	1.037	1.002	1.020	1.070
Width of paunch divided by width of fore chest—ratio	1.499	1.569	1.490	1.529	1.481	1.705	1.633	1.558	1.198	1.426	1.312	1.209
Circumference of paunch divided by circumference of fore chest—ratio	1.142	1.168	1.159	1.194	1.146	1.200	1.265	1.182	1.103	1.190	1.147	1.135
Contour area of paunch divided by contour area of fore chest—ratio	1.538	1.590	1.529	1.575	1.486	1.680	1.810	1.601	1.256	1.502	1.379	1.241

In addition to the ante-mortem measurements given in table 5 a number of additional values have been derived to show more completely the differences in the conformation of the Herefords, the Holsteins, and the Aberdeen Angus. The methods employed in obtaining the contours, body surface area, volume of barrel, angle of rump, thoracic and abdominal indexes, legginess, and wedge shape are explained in detail in a previous publication (*9*). These supplemental ante-mortem data are given in table 7.

Attention is again called to the fact that the Holsteins and the Aberdeen Angus were older than the Herefords at the time of slaughter and that this greater maturity probably had an effect on the absolute values representing total area of fore chest and of paunch, body surface area, and volume of barrel. A marked progressive increase is shown from Hereford to Holstein to Aberdeen Angus in the average values for total contour area of both fore chest and paunch. In the fore-chest contours, slightly more than half the area is above the vertical midpoint for Herefords and for the Aberdeen Angus, whereas very slightly more than half was below for the Holsteins. In the paunch slightly more than half of the total area was below the vertical midpoint for all three groups. In both fore chest and paunch, the values obtained by dividing the total contour area by the corresponding depth, width, and circumference, progress with considerable regularity from Herefords to Holsteins to Aberdeen Angus. However, the increase is less marked from Holsteins to Aberdeen Angus in the case of circumference of paunch, than for the others.

The body surface area is much less for the Herefords than for the Holsteins, but almost the same for the Aberdeen Angus as for the Holsteins. A similar relationship of values exists for the estimated volume of barrel. Though perhaps not highly significant, the angle of rump was highest for the Holsteins and lowest for the Aberdeen Angus. The thoracic index decreases with considerable regularity from Herefords to Holsteins to Aberdeen Angus, signifying that the Holsteins were intermediate and that the Aberdeen Angus was the highest in proportion of width to depth of fore chest. Values for abdominal index are nearly the same for all three breeds. The legginess was almost the same for the Holsteins as for the Herefords, but distinctly less for the Aberdeen Angus.

On the basis of actual measurements, the Herefords had almost no vertical wedge shape, as determined by subtracting depth of fore chest from depth of paunch; the Holsteins had more than 10 times as much as the Herefords; and the Aberdeen Angus had more than 3 times as much as the Holsteins. In width, the wedge shape decreased markedly from Herefords to Holsteins to Aberdeen Angus, showing that the Herefords were narrowest in the chest as compared with the width of paunch. In circumference the wedge shape was almost the same for all three breeds; and on the basis of the contour areas the wedge shape of the Herefords and Holsteins was almost identical, but that of the Aberdeen Angus was considerably less.

Another method of showing wedge shape is to divide the paunch measurement by the corresponding fore-chest measurement. The ratios for depth obtained in this manner increase somewhat from Herefords to Holsteins and to a greater extent from Holsteins to Aberdeen Angus. On the other hand, the corresponding ratios for widths decrease. Ratios for circumferences are highest for the

Herefords, but those for Holsteins and for Aberdeen Angus are nearly the same. For contour areas a decrease in ratios is shown from Herefords to Holsteins to Aberdeen Angus. The ratios show practically the same thing as the differences in measurements, indicating that the Herefords were relatively shallow in the paunch, whereas the Holsteins had somewhat greater and the Aberdeen Angus much greater relative paunch depth; that in width the Herefords were relatively narrow-chested, whereas the Holsteins had greater and the Aberdeen Angus still greater relative width of fore chest; that in circumference the relation of paunch to fore chest was more nearly the same for all breeds and that in contour area the relation of paunch to fore chest was lower for the Aberdeen Angus than for the Holsteins, and lower for both than for the Herefords. The data in table 7 emphasize again the effect of fleshing on the body proportions of the animal.

POST-MORTEM ANATOMICAL DATA

The seven Herefords were slaughtered during the period of June 17 to 21, 1929, and post-mortem data were obtained in accordance with the general plan adopted by the Bureau of Dairy Industry for studying the relation between the conformation and anatomy of the dairy cow and her milk- and butterfat-producing capacity. The post-mortem data for the Herefords, the Holsteins, and the Aberdeen Angus are presented in table 8. The live weights differ somewhat from those shown in the ante-mortem data as they were taken immediately before slaughter, whereas the ante-mortem data sometimes were obtained several days earlier. Empty body weight is used to represent the net weight of the total animal structure. It is determined by subtracting the total weight of the contents of the stomachs and intestines from the live weight. It is more significant than live weight as it eliminates variations in weight due to the "fill" of the animal. The other items are self-explanatory.

In table 8, data are given for each animal in the units of weight or measurement as taken, and show the differences existing between individuals or breeds in the size of the animal or its organs and body parts. Here, again, the authors call attention to the possible effect of age differences on these absolute values and on comparisons based upon them. The values designated as "units per 100 pounds of empty body weight", show the relation of each organ and body part to the weight of total animal structure.

The actual values for Holsteins are greater than those for Herefords in all but 3 of the 67 items compared. The actual values for the Aberdeen Angus are higher than those for the Herefords in all but 4 of the 34 items compared, but greater than those for the Holsteins in only 11 of the 34. When compared on the basis of the values showing size of organ or body part in relation to empty body weight, the Herefords exceed the Holsteins in 53 of the 66 items compared, and the Herefords exceed the Aberdeen Angus in 26 of the 33 items compared. The Holsteins exceed the Aberdeen Angus in 27 of the 33 items compared. To obtain a better idea of the degree of difference between the breeds, both the actual units and the values based on empty body weight are compared, as in the case of the ante-mortem data, by reducing the differences to a percentage basis. The percentages for the different comparisons for each item are shown in table 9.

TABLE 8.—*Post-mortem data on the animals used in the experiments*

Item	Herefords								Holsteins			Aberdeen Angus
	Group 1 (dairy management)				Group 2 (beef management)			Average	No. 299	No. 827	Average	A-300
	H-2	H-5	H-6	H-16	H-1	H-4	H-17					
Live weight:												
Actual weight, pounds	795	735	790	935	570	805	1,095	818	1,420	1,338	1,379	1,585
Units per 100 pounds empty body weight	115.64	123.20	127.47	117.07	125.56	121.36	117.37	121.10	114.81	113.78	114.30	107.36
Empty body weight:												
Actual weight, pounds	687.45	596.60	619.75	798.65	453.95	663.30	932.95	678.95	1,236.85	1,175.94	1,206.40	1,476.36
Weight of blood:												
Actual weight, do	30.25	23.75	24.00	27.25	----------	24.75	36.75	27.79	62.00	48.75	55.38	----------
Units per 100 pounds empty body weight	4.40	3.98	3.87	3.41	----------	3.73	3.94	3.89	5.01	4.15	4.58	----------
Weight of thyroid:												
Actual weight, grams	21.0	11.5	12.5	19.0	12.2	----------	----------	15.24	39.0	40.4	39.70	57.50
Units per 100 pounds empty body weight	3.05	1.93	2.02	2.38	2.69	----------	----------	2.41	3.15	3.44	3.30	3.89
Weight of brain:												
Actual weight, grams	406.0	341.0	385.0	353.0	325.5	326.5	362.4	357.06	454.0	507.0	480.50	----------
Units per 100 pounds empty body weight	59.06	57.16	62.12	44.20	71.70	49.22	38.84	54.61	36.71	43.11	39.91	----------
Weight of pituitary body:												
Actual weight, grams	2.50	2.00	2.00	2.10	1.70	2.50	2.50	2.19	4.20	3.23	3.72	----------
Units per 100 pounds empty body weight	0.36	0.34	0.32	0.26	0.37	0.38	0.27	0.33	0.34	0.27	0.31	----------
Weight of udder (empty):												
Actual weight, pounds	9.95	7.15	8.35	14.50	6.30	6.35	18.00	10.09	30.50	22.00	26.25	44.00
Units per 100 pounds empty body weight	1.45	1.20	1.35	1.82	1.39	0.96	1.93	1.44	2.47	1.87	2.17	2.98
Weight of hide:												
Actual weight, pounds	64.00	66.00	72.00	64.00	54.00	62.00	65.00	63.86	79.75	81.43	80.59	82.50
Units per 100 pounds empty body weight	9.31	11.06	11.62	8.01	11.90	9.35	6.97	9.75	6.45	6.92	6.69	5.59
Weight of genital organs:												
Actual weight, pounds	21.70	3.40	5.75	77.50	1.20	6.15	98.25	30.56	3.60	3.05	3.33	2.95
Units per 100 pounds empty body weight	3.16	0.57	0.93	9.70	0.26	0.93	10.53	3.73	0.29	0.26	0.28	0.20
Weight of ovaries:												
Actual weight, grams	11.0	9.2	15.2	17.0	7.0	11.7	13.5	12.09	37.2	14.1	25.65	34.40
Units per 100 pounds empty body weight	1.60	1.54	2.45	2.13	1.54	1.76	1.45	1.78	3.01	1.20	2.11	2.33
Weight of amniotic fluid:												
Actual weight, grams	2,790	378	959	6,532	----------	255	6,078	2,832	----------	----------	----------	----------
Units per 100 pounds empty body weight	405.85	63.36	154.74	817.88	----------	38.44	651.48	355.29	----------	----------	----------	----------
Weight of fetus:												
Actual weight, grams	3,561	46	192	17,464	----------	236	27,443	8,157	----------	----------	----------	----------
Units per 100 pounds empty body weight	518.00	7.71	30.98	2,186.69	----------	35.58	2,941.53	953.42	----------	----------	----------	----------
Period of gestation, days	157	73	91	223	(1)	(2)	271	----------	(1)	(1)	----------	(1)

[1] Not pregnant.

[2] Period of gestation not known.

TABLE 8.—*Post-mortem data on the animals used in the experiments*—Continued

Item	Herefords								Holsteins			Aberdeen Angus
	Group 1 (dairy management)				Group 2 (beef management)			Average	No. 299	No. 827	Average	A-300
	H-2	H-5	H-6	H-16	H-1	H-4	H-17					
Weight fetal membranes:												
Actual weight.....grams..	1,134	266	332	3,629	.....	55	.....	1,083.2	.....	.....	.....	.....
Units per 100 pounds empty body weight.....	164.96	44.59	53.57	454.39	.....	8.29	.....	145.16	.....	.....	.....	.....
Weight of liver:												
Actual weight.....pounds..	9.55	7.00	8.95	7.60	6.05	9.40	10.40	8.42	16.95	13.85	15.40	14.75
Units per 100 pounds empty body weight.....	1.39	1.17	1.44	0.95	1.33	1.42	1.11	1.26	1.37	1.18	1.28	1.00
Weight of spleen:												
Actual weight.....grams..	645.0	478.5	533.0	572.0	386.0	500.5	809.0	560.57	1,058.0	632.0	845.00	839.20
Units per 100 pounds empty body weight.....	93.83	80.20	86.00	71.62	85.03	75.46	86.71	82.69	85.54	53.74	69.64	56.84
Weight of pancreas:												
Actual weight.....grams..	261.5	160.0	239.5	208.5	146.2	.....	231.7	207.90	582.5	508.5	545.50	371.00
Units per 100 pounds empty body weight.....	38.04	26.82	38.64	26.11	32.21	.....	24.84	31.11	47.10	43.24	45.17	25.13
Length of small intestine:												
Actual measurement.....feet..	120.87	113.16	112.50	112.34	93.15	112.67	127.26	113.14	171.54	144.22	157.88	140.22
Units per 100 pounds empty body weight.....	17.58	18.97	18.15	14.07	20.52	16.99	13.64	17.13	13.87	12.26	13.07	9.50
Length of large intestine:												
Actual measurement.....feet..	31.98	30.50	29.85	30.60	23.45	26.73	37.06	30.02	45.92	43.16	44.54	41.49
Units per 100 pounds empty body weight.....	4.65	5.11	4.82	3.83	5.17	4.03	3.97	4.51	3.71	3.67	3.69	2.81
Total length of intestines:												
Actual measurement.....feet..	152.85	143.66	142.35	142.94	116.60	139.40	164.32	143.16	217.46	187.38	202.42	181.71
Units per 100 pounds empty body weight.....	22.23	24.08	22.97	17.90	25.69	21.02	17.61	21.64	17.58	15.93	16.76	12.31
Weight of small intestine:												
Actual weight.....pounds..	11.10	10.35	9.35	9.20	9.50	10.60	12.36	10.34	13.25	9.75	11.50	8.70
Units per 100 pounds empty body weight.....	1.61	1.73	1.51	1.15	2.09	1.60	1.32	1.57	1.07	0.83	0.95	0.59
Weight of large intestine:												
Actual weight.....pounds..	10.35	9.30	7.85	10.50	7.10	11.60	12.50	9.89	9.90	8.05	8.98	7.75
Units per 100 pounds empty body weight.....	1.51	1.56	1.27	1.31	1.56	1.75	1.34	1.47	0.80	0.68	0.74	0.52
Total weight of intestines:												
Actual weight.....pounds..	21.45	19.65	17.20	19.70	16.60	22.20	24.80	20.23	23.15	17.80	20.48	16.45
Units per 100 pounds empty body weight.....	3.12	3.29	2.78	2.47	3.66	3.35	2.66	3.05	1.87	1.51	1.69	1.11
Weight of paunch:												
Actual weight.....pounds..	13.00	11.60	12.70	10.95	8.65	13.20	15.10	12.17	24.85	16.65	20.75	14.95
Units per 100 pounds empty body weight.....	1.89	1.94	2.05	1.37	1.91	1.99	1.62	1.82	2.01	1.42	1.72	1.01
Weight of reticulum:												
Actual weight.....pounds..	2.30	1.95	1.75	2.25	1.60	2.05	2.10	2.00	3.70	2.53	3.12	2.85
Units per 100 pounds empty body weight.....	0.33	0.33	0.28	0.28	0.35	0.31	0.23	0.30	0.30	0.22	0.26	0.19

Weight of omasum:												
Actual weight	pounds	8.45	7.60	7.45	7.85	4.70	6.95	8.40	7.34	13.50	9.33	11.42	8.80
Units per 100 pounds empty body weight		1.23	1.27	1.20	0.98	1.04	1.05	0.90	1.10	1.09	0.79	0.94	0.60
Weight of abomasum:													
Actual weight	pounds	3.55	2.95	4.00	3.85	5.05	3.90	4.45	3.96	4.90	3.28	4.09	4.75
Units per 100 pounds empty body weight		0.52	0.49	0.65	0.48	1.11	0.59	0.48	0.62	0.40	0.28	0.34	0.32
Total weight stomachs:													
Actual weight	pounds	27.30	24.10	25.90	24.90	20.00	26.10	30.05	25.48	46.95	31.79	39.37	31.35
Units per 100 pounds empty body weight		3.97	4.04	4.18	3.12	4.41	3.93	3.22	3.84	3.80	2.70	3.25	2.12
Total weight of abdominal fat:													
Actual weight	pounds	13.30	7.70	8.75	24.55	3.95	9.35	19.65	12.46	46.10	81.10	63.60	87.15
Units per 100 pounds empty body weight		1.93	1.29	1.41	3.07	0.87	1.41	2.11	1.73	3.73	6.90	5.32	5.90
Weight of pluck:													
Actual weight	pounds	----------	11.25	12.45	15.35	9.75	12.70	15.55	12.84	27.55	29.20	28.38	26.50
Units per 100 pounds empty body weight		----------	1.89	2.01	1.92	2.15	1.91	1.67	1.93	2.23	2.48	2.36	1.80
Weight of right lung:													
Actual weight	pounds	2.85	2.70	2.80	3.15	2.60	2.85	2.90	2.84	5.40	4.80	5.10	3.15
Units per 100 pounds empty body weight		0.41	0.45	0.45	0.39	0.57	0.43	0.31	0.43	0.44	0.41	0.43	0.21
Weight left lung:													
Actual weight	pounds	2.20	2.00	2.20	2.50	1.90	2.15	2.25	2.17	4.20	3.30	3.75	2.70
Units per 100 pounds empty body weight		0.32	0.34	0.35	0.31	0.42	0.32	0.24	0.33	0.34	0.28	0.31	0.18
Total weight lungs:													
Actual weight	pounds	5.05	4.70	5.00	5.65	4.50	5.00	5.15	5.01	9.60	8.10	8.85	5.85
Units per 100 pounds empty body weight		0.73	0.79	0.81	0.71	0.99	0.75	0.55	0.76	0.78	0.69	0.74	0.40
Weight heart, auricles attached:													
Actual weight	pounds	2.50	2.25	2.50	2.80	1.95	2.60	3.05	2.52	5.55	4.70	5.13	4.30
Units per 100 pounds empty body weight		0.36	0.38	0.40	0.35	0.43	0.39	0.33	0.38	0.45	0.40	0.43	0.29
Circumference heart (base):													
Actual measurement	centimeters	41.00	----------	40.50	41.00	36.50	40.75	43.00	40.46	51.60	51.80	51.70	51.00
Units per 100 pounds empty body weight		5.96	----------	6.53	5.13	8.04	6.14	4.61	6.07	4.17	4.40	4.29	3.45
Circumference heart (apex 1):													
Actual measurement	centimeters	41.00	----------	42.00	41.00	38.25	41.50	44.00	41.29	54.30	51.35	52.83	48.50
Units per 100 pounds empty body weight		5.96	----------	6.78	5.13	8.43	6.26	4.72	6.21	4.39	4.37	4.38	3.29
Circumference heart (apex 2):													
Actual measurement	centimeters	45.75	----------	48.75	47.00	44.00	48.50	49.00	47.17	63.35	59.15	61.25	55.00
Units per 100 pounds empty body weight		6.66	----------	7.87	5.88	9.69	7.31	5.25	7.11	5.12	5.03	5.08	3.73
Weight heart, auricles removed:													
Actual weight	pounds	2.30	2.00	2.30	2.55	1.75	2.40	2.75	2.29	5.05	4.25	4.65	3.90
Units per 100 pounds empty body weight		0.33	0.34	0.37	0.32	0.39	0.36	0.29	0.34	0.41	0.36	0.39	0.26
Total weight of thoracic fat:													
Actual weight	pounds	2.25	1.90	1.70	3.30	0.45	1.25	3.65	2.07	4.60	11.50	8.05	8.75
Units per 100 pounds empty body weight		0.33	0.32	0.27	0.41	0.10	0.19	0.39	0.29	0.37	0.98	0.68	0.59
Weight of kidneys:													
Actual weight	grams	740.00	626.00	581.70	670.00	547.50	779.00	757.50	671.67	1,313.00	1,094.50	1,203.75	1,746.40
Units per 100 pounds empty body weight		107.64	104.93	93.86	83.89	120.61	117.44	81.19	101.37	106.16	93.07	99.62	118.30
Weight of adrenals:													
Actual weight	grams	16.50	17.50	21.00	14.50	19.70	19.80	20.2	18.46	36.5	24.00	30.25	57.50
Units per 100 pounds empty body weight		2.40	2.93	3.39	1.82	4.34	2.99	2.17	2.86	2.95	2.04	2.50	3.89
Weight of dressed carcass:													
Actual weight	pounds	398.00	378.00	638.00	464.00	274.00	420.00	538.00	408.57	773.00	734.50	753.75	----------
Units per 100 pounds empty body weight		57.90	63.36	82.61	58.10	60.36	63.32	57.67	60.47	62.50	62.46	62.48	----------

TABLE 8.—*Post-mortem data on the animals used in the experiments*—Continued

Item	Herefords								Holsteins			Aberdeen Angus
	Group 1 (dairy management)				Group 2 (beef management)			Average	No. 299	No. 827	Average	A-300
	H-2	H-5	H-6	H-16	H-1	H-4	H-17					
Depth thoracic cavity:												
First thoracic vertebra:												
Actual measurement.....centimeters..	16.00	16.00	13.25	15.25	14.00	12.50	17.50	14.93	20.00	17.50	18.75	.....
Units per 100 pounds empty body weight...	2.33	2.68	2.14	1.91	3.08	1.88	1.88	2.27	1.62	1.49	1.56	.....
Second thoracic vertebra:												
Actual measurement.....centimeters..	22.00	22.25	21.00	22.75	20.00	20.25	24.25	21.79	29.00	20.50	24.75	.....
Units per 100 pounds empty body weight...	3.20	3.73	3.39	2.85	4.41	3.05	2.60	3.32	2.34	1.74	2.04	.....
Third thoracic vertebra:												
Actual measurement.....centimeters..	28.00	27.25	27.25	28.75	26.00	25.75	29.00	27.43	36.25	30.50	33.38	.....
Units per 100 pounds empty body weight...	4.07	4.57	4.40	3.60	5.73	3.88	3.11	4.19	2.93	2.59	2.76	.....
Fourth thoracic vertebra:												
Actual measurement.....centimeters..	31.75	33.25	33.00	34.25	31.25	31.25	34.75	32.79	43.75	36.75	40.25	.....
Units per 100 pounds empty body weight...	4.62	5.57	5.32	4.29	6.88	4.71	3.72	5.02	3.54	3.13	3.34	.....
Fifth thoracic vertebra:												
Actual measurement.....centimeters..	36.50	36.25	36.50	37.25	35.00	36.50	38.00	36.57	47.00	40.75	43.88	.....
Units per 100 pounds empty body weight...	5.31	6.08	5.89	4.66	7.71	5.50	4.07	5.60	3.80	3.47	3.64	.....
Sixth thoracic vertebra:												
Actual measurement.....centimeters..	39.00	38.75	39.50	39.00	37.75	40.25	39.75	39.14	49.50	44.25	46.88	.....
Units per 100 pounds empty body weight...	5.67	6.50	6.37	4.88	8.32	6.07	4.26	6.01	4.00	3.76	3.88	.....
Seventh thoracic vertebra:												
Actual measurement.....centimeters..	42.00	41.50	41.50	41.25	39.50	41.75	41.75	41.32	51.75	46.75	49.25	.....
Units per 100 pounds empty body weight...	6.11	6.96	6.70	5.16	8.70	6.29	4.48	6.34	4.18	3.98	4.08	.....
Eighth thoracic vertebra:												
Actual measurements.....centimeters..	44.00	43.00	43.50	42.50	42.00	43.75	43.25	43.14	53.75	49.50	51.63	.....
Units per 100 pounds empty body weight...	6.40	7.21	7.02	5.32	9.25	6.60	4.64	6.63	4.35	4.21	4.28	.....
Ninth thoracic vertebra:												
Actual measurement.....centimeters..	44.25	43.25	42.00	42.50	43.25	43.75	43.00	43.14	52.50	51.00	51.75	.....
Units per 100 pounds empty body weight...	6.44	7.25	6.78	5.32	9.53	6.60	4.61	6.65	4.24	4.34	4.29	.....
Tenth thoracic vertebra:												
Actual measurement.....centimeters..	41.25	42.00	41.00	40.25	42.75	43.50	*39.50	41.46	48.75	48.50	48.63	.....
Units per 100 pounds empty body weight..	6.00	7.04	6.62	5.04	9.42	6.56	4.23	6.42	3.94	4.12	4.03	.....
Eleventh thoracic vertebra:												
Actual measurement.....centimeters..	38.00	38.00	37.00	35.75	41.00	39.50	36.25	37.93	44.75	43.50	44.13	.....
Units per 100 pounds empty body weight...	5.53	6.37	5.97	4.48	9.03	5.96	3.89	5.89	3.62	3.70	3.66	.....
Twelfth thoracic vertebra:												
Actual measurement.....centimeters..	31.50	33.75	30.75	28.50	37.25	34.00	28.50	32.04	40.75	38.00	39.38	.....
Units per 100 pounds empty body weight...	4.58	5.66	4.96	3.57	8.21	5.13	3.05	5.02	3.29	3.23	3.26	.....
Thirteenth thoracic vertebra:												
Actual measurement.....centimeters..	21.25	25.25	21.25	12.50	33.50	25.50	11.75	21.57	21.00	18.00	19.50	.....
Units per 100 pounds empty body weight...	3.09	4.23	3.43	1.57	7.38	3.84	1.26	3.54	1.70	1.53	1.62	.....

Maximum length thoracic cavity:												
Actual measurement.....centimeters	68.75	70.50	67.00	71.00	59.75	69.75	69.50	68.04	81.75	81.25	81.50	
Units per 100 pounds empty body weight	10.00	11.82	10.81	8.89	13.16	10.52	7.45	10.38	6.61	6.91	6.76	
Width thoracic cavity:												
At first rib:												
Actual measurement.....centimeters	8.20	8.80	8.40	8.30	8.10	8.40	8.70	8.41	10.60	9.60	10.10	
Units per 100 pounds empty body weight	1.19	1.48	1.36	1.04	1.78	1.27	0.93	1.29	0.86	0.82	0.84	
At second rib:												
Actual measurement.....centimeters	10.30	10.60	10.90	10.60	10.40	10.70	11.00	10.64	13.20	11.80	12.50	
Units per 100 pounds empty body weight	1.50	1.78	1.76	1.33	2.29	1.61	1.18	1.64	1.07	1.00	1.04	
At third rib:												
Actual measurement.....centimeters	13.10	13.40	14.40	14.20	14.20	14.10	14.70	14.01	17.50	15.70	16.60	
Units per 100 pounds empty body weight	1.91	2.25	2.32	1.78	3.13	2.13	1.58	2.16	1.41	1.34	1.38	
At fourth rib:												
Actual measurement.....centimeters	17.30	17.10	18.70	18.40	18.30	17.70	19.30	18.11	23.00	20.50	21.75	
Units per 100 pounds empty body weight	2.52	2.87	3.02	2.30	4.03	2.67	2.07	2.78	1.86	1.74	1.80	
At fifth rib:												
Actual measurement.....centimeters	21.30	21.00	22.50	23.00	21.90	21.30	24.10	22.16	28.70	25.40	27.05	
Units per 100 pounds empty body weight	3.10	3.52	3.63	2.88	4.82	3.21	2.58	3.39	2.32	2.16	2.24	
At sixth rib:												
Actual measurement.....centimeters	25.10	25.10	26.10	27.90	25.70	24.80	28.70	26.20	34.60	30.80	32.70	
Units per 100 pounds empty body weight	3.65	4.21	4.21	3.49	5.66	3.74	3.08	4.01	2.80	2.62	2.71	
At seventh rib:												
Actual measurement.....centimeters	30.40	29.00	29.70	35.70	29.50	28.70	35.40	30.91	41.00	36.20	38.60	
Units per 100 pounds empty body weight	4.42	4.86	4.79	4.22	6.50	4.33	3.79	4.70	3.31	3.08	3.20	
At eighth rib:												
Actual measurement.....centimeters	35.30	32.80	32.80	39.60	32.90	32.70	40.20	35.19	46.30	41.70	44.00	
Units per 100 pounds empty body weight	5.13	5.50	5.29	4.96	7.25	4.93	4.31	5.34	3.74	3.55	3.65	
At ninth rib:												
Actual measurement.....centimeters	36.70	35.20	34.90	42.50	33.80	36.00	43.30	37.49	49.10	45.10	47.10	
Units per 100 pounds empty body weight	5.34	5.90	5.63	5.32	7.45	5.43	4.64	5.67	3.97	3.84	3.91	
Diameter of trachea outside fifth ring:												
Actual measurement.....centimeters		4.52	4.09		4.25			4.29	5.17	4.56	4.87	
Units per 100 pounds empty body weight		0.76	0.66		0.94			0.79	0.42	0.39	0.41	
Diameter of trachea inside fifth ring:												
Actual measurement.....centimeters		3.47	3.12		3.51			3.37	4.28	3.78	4.03	
Units per 100 pounds empty body weight		0.58	0.50		0.77			0.62	0.35	0.32	0.34	
Area of trachea inside fifth ring:												
Actual measurement.....square centimeters		9.20	10.00		9.00			9.40	12.90	10.73	11.82	
Units per 100 pounds empty body weight		1.54	1.61		1.98			1.71	1.04	0.91	0.98	
Diameter of trachea outside fourth ring:												
Actual measurement.....centimeters	3.48	4.52	4.11		4.27			4.10	5.21	4.63	4.92	
Units per 100 pounds empty body weight	0.51	0.76	0.66		0.94			0.72	0.42	0.39	0.41	
Diameter of trachea inside fourth ring:												
Actual measurement.....centimeters	2.64	3.50	3.19		3.61			3.24	4.28	3.80	4.04	
Units per 100 pounds empty body weight	0.38	0.59	0.51		0.80			0.57	0.35	0.32	0.34	
Area of trachea inside fourth ring:												
Actual measurement.....square centimeters	7.30	9.83			9.10			8.74	13.17	11.60	12.39	
Units per 100 pounds empty body weight	1.06	1.65			2.00			1.57	1.06	0.99	1.03	
Weight of thymus:												
Actual weight.....grams									127.0	261.5	194.25	
Units per 100 pounds empty body weight									10.27	22.24	16.26	

TABLE 9.—*Comparative anatomy of the Herefords, Holsteins, and Aberdeen Angus*

Item	Actual units			Units per 100 pounds of empty body weight		
	Relation of Holsteins to Herefords	Relation of Aberdeen Angus to Herefords	Relation of Aberdeen Angus to Holsteins	Relation of Holsteins to Herefords	Relation of Aberdeen Angus to Herefords	Relation of Aberdeen Angus to Holsteins
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Live weight	+68.58	+93.77	+14.94	−5.62	−11.35	−6.07
Empty body weight	+77.69	+117.44	+22.37			
Weight of blood	+99.28			+17.74		
Weight of thyroid	+160.50	+277.30	+44.84	+36.93	+61.41	+17.88
Weight of brain	+34.57			−26.92		
Weight of pituitary body	+69.86			−6.06		
Weight of udder (empty)	+160.16	+336.08	+67.62	+50.69	+106.94	+37.33
Weight of hide	+26.20	+29.19	+2.37	−31.38	−42.67	−16.44
Weight of genital organs	−89.10	−90.35	−11.41	−92.49	−94.64	−28.57
Weight of ovaries	+112.16	+184.53	+34.11	+18.54	+30.90	+10.43
Weight of liver	+82.90	+75.18	−4.22	+1.59	−20.63	−21.87
Weight of spleen	+50.74	+49.70	−.69	−15.78	−31.26	−18.38
Weight of pancreas	+162.39	+78.45	−31.99	+45.19	−19.22	−44.37
Length of small intestine	+39.54	+23.93	−11.19	−23.70	−44.54	−27.31
Length of large intestine	+48.37	+38.21	−6.85	−18.18	−37.69	−23.85
Total length of intestines	+41.39	+26.93	−10.23	−22.55	−43.11	−26.55
Weight of small intestine	+11.12	−15.86	−24.35	−39.49	−62.42	−37.89
Weight of large intestine	−9.20	−21.64	−13.70	−49.66	−64.63	−29.73
Total weight of intestines	+1.24	−18.69	−19.68	−44.59	−63.61	−34.32
Weight of paunch	+70.50	+22.84	−27.95	−5.49	−44.51	−41.28
Weight of reticulum	+56.00	+42.50	−8.65	−13.33	−36.67	−26.92
Weight of omasum	+55.59	+19.89	−22.94	−14.55	−45.45	−36.17
Weight of abomasum	+3.28	+19.95	+16.14	−45.16	−48.39	−5.88
Total weight of stomachs	+54.51	+23.04	−20.37	−15.36	−44.79	−34.77
Total weight of abdominal fat	+410.43	+599.44	+37.03	+207.51	+241.04	+10.90
Weight of pluck	+121.03	+106.39	−6.62	+22.28	−6.74	−23.73
Weight of right lung	+79.58	+10.92	−38.24	−.00	−51.16	−51.16
Weight of left lung	+72.81	+24.42	−28.00	−6.06	−45.45	−41.94
Total weight of lungs	+76.65	+16.77	−33.90	−2.63	−47.37	−45.95
Weight of heart, auricles attached	+103.57	+70.63	−16.18	+13.16	−23.68	−32.56
Circumference of heart (base)	+27.78	+26.05	−1.35	−29.32	−43.16	−19.58
Circumference of heart (apex 1)	+27.95	+17.46	−8.20	−29.47	−47.02	−24.89
Circumference of heart (apex 2)	+29.85	+16.60	−10.20	−28.55	−47.54	−26.57
Weight of heart, auricles removed	+103.06	+70.31	−16.13	+14.71	−23.53	−33.33
Total weight of thoracic fat	+288.89	+322.71	+8.70	+134.48	+103.45	−13.24
Weight of kidneys	+79.22	+160.00	+45.08	−1.73	+16.70	+18.75
Weight of adrenals	+63.87	+211.48	+90.08	−12.59	+36.01	+55.60
Weight of dressed carcass	+84.48			+3.32		
Depth of thoracic cavity:						
At first thoracic vertebra	+25.59			−31.28		
At second thoracic vertebra	+13.58			−38.55		
At third thoracic vertebra	+21.69			−34.13		
At fourth thoracic vertebra	+22.75			−33.47		
At fifth thoracic vertebra	+19.99			−35.00		
At sixth thoracic vertebra	+19.78			−35.44		
At seventh thoracic vertebra	+19.19			−35.65		
At eighth thoracic vertebra	+19.68			−35.44		
At ninth thoracic vertebra	+19.96			−35.49		
At tenth thoracic vertebra	+17.29			−37.23		
At eleventh thoracic vertebra	+16.35			−37.86		
At twelfth thoracic vertebra	+22.91			−35.06		
At thirteenth thoracic vertebra	−9.60			−54.24		
Maximum length of thoracic cavity	+19.78			−34.87		
Width of thoracic cavity:						
At first rib	+20.10			−34.88		
At second rib	+17.48			−36.59		
At third rib	+18.49			−36.11		
At fourth rib	+20.10			−35.25		
At fifth rib	+22.07			−33.92		
At sixth rib	+24.81			−32.42		
At seventh rib	+24.88			−31.91		
At eighth rib	+25.04			−31.65		
At ninth rib	+25.63			−31.04		
Diameter of trachea outside fifth ring	+13.52			−48.10		
Diameter of trachea inside fifth ring	+19.58			−45.16		
Area of trachea inside fifth ring	+25.74			−42.69		
Diameter of trachea outside fourth ring	+20.00			−43.06		
Diameter of trachea inside fourth ring	+24.69			−40.35		
Area of trachea inside fourth ring	+41.76			−34.39		

PERCENTAGE DIFFERENCE IN ACTUAL UNITS OF WEIGHT OR MEASUREMENT

The percentages in table 9 indicate that on the basis of actual units, the Holsteins exceeded the Herefords by more than 100 percent in nine items, the greatest differences being, in order of magnitude, weights of total abdominal fat, total thoracic fat, pancreas, thyroid, udder, pluck,[4] ovaries, and the two weights of the heart. The only items differing by less than 10 percent are weights of total intestine, abomasum, and large intestine, and one of the depths of the thoracic cavity.

The Aberdeen Angus exceeded the Herefords by more than 100 percent for nine items. Three of these (the weights of total abdominal fat, total thoracic fat, and the udder) were above 300 percent. In this connection an extremely fatty condition of the udder is noted, indicating that the greatest differences are in the parts made up chiefly of body fat. Two others (the weights of thyroid and of adrenals) were above 200 percent, suggesting a marked difference in some of the endocrine glands. The other four in the order of magnitude are weights of ovaries, kidneys, empty body, and pluck. Deposition of fat could have been at least partly responsible for the high percentage of each of these nine items, except for the weight of ovaries. None of the items in this comparison had a percentage below 10 percent. Of the five smallest percentages, which ranged from 10.92 for weight of right lung to 17.46 for circumference of heart, four were for weights or measurements of organs of circulation and respiration.

When the Aberdeen Angus is compared with the Holsteins the differences are much less marked. In no case is the difference as much as 100 percent. The four highest percentages, all of which show excesses for the Aberdeen Angus, range from 90.08 to 44.84 and include in the order of their magnitude the weights of adrenals, udder, kidneys, and thyroid. On the other hand nine items differ by less than 10 percent and only two of them are greater for the Aberdeen Angus than for the Holsteins.

In comparing the Aberdeen Angus cow with cows of the other breeds—especially the Herefords—the extreme differences in condition of flesh should be kept in mind. Undoubtedly these differences in flesh are responsible for some of the differences found in both the ante-mortem and post-mortem data.

PERCENTAGE DIFFERENCES IN UNITS OF WEIGHT OR MEASUREMENT PER 100 POUNDS OF EMPTY BODY WEIGHT

When the comparison of breeds was made on the basis of units per 100 pounds of empty body weight, the Holsteins differed from the Herefords by as much as 100 percent only for weight of abdominal and thoracic fats. Both were greater for the Holsteins than for the Herefords. For nine items the difference was less than 10 percent. Of these, six were greater for the Herefords. Values that were lower for Holsteins than for Herefords on the basis of actual units became even lower on this basis, and those that were positive on the actual unit basis showed either lower positive or negative values when compared on the basis of empty body weight. The effect of degree of fleshing on the empty body weight may have been to some extent responsible for these differences between the two bases of comparison.

[4] In this study the word "pluck" refers to the unseparated contents of the thoracic cavity as removed in slaughtering.

A comparison of the Aberdeen Angus with the Herefords shows only three items (weight of abdominal and thoracic fats and the udder) differing by more than 100 percent, all of which are lower for the Herefords than for the Aberdeen Angus. Only one item (the weight of pluck) differs by less than 10 percent. As in comparing the Holsteins with the Herefords, all items that were positive on the basis of actual units became either lower positive or negative, and those that were negative became negative to an even greater degree. Deposition of fat, or fleshing, seems to have been chiefly responsible for the differences shown by the two methods of comparison.

A comparison of the Aberdeen Angus with the Holsteins shows that no item of measurement differs by as much as 60 percent, only two differ by more than 50 percent, and only two differ by less than 10 percent. The relation between the values based on actual units and those based on units per 100 pounds of empty body weight in this breed comparison is similar to that shown in the other breed comparisons and the same factors are probably responsible.

PERCENTAGE DIFFERENCES IN GROUPS OF ITEMS COMBINED ON THE BASIS OF ANATOMY AND FUNCTION

To obtain an idea of the extent to which differences in anatomy are associated with the functions of the organs and body parts, the items in table 9 were divided into seven groups as follows: (1) The body-size group (skeletal and muscular), which includes the live weight, empty body weight, weight of hide and dressed carcass, and the carcass measurements; (2) the nervous-system group, which includes the weight of brain; (3) the circulation and respiration group, which includes weight of blood, pluck, lungs, and heart, and the measurements of the heart and trachea; (4) the digestion group, which includes the weight of liver, pancreas, intestines and stomachs, and the intestine measurements; (5) the urogenital group, which includes the weight of udder, genital organs, ovaries, and kidneys; (6) the endocrine gland group, which includes the weight of the thyroid, pituitary body, spleen, and adrenals; and (7) the visceral fats group, which includes the abdominal and thoracic fats.

The average of the differences expressed in percentage for the items in each group and for each breed comparison, was determined first with the plus and minus signs disregarded, and second with the plus and minus signs considered. The averages are given in table 10.

The organs and parts of the Holsteins and the Aberdeen Angus were actually of greater magnitude than those of the Herefords for all groups, whereas those of the Aberdeen Angus were smaller than those of the Holsteins in the circulation and respiration and the digestion groups. However, on the basis of units per 100 pounds of empty body weight, which measures the proportion of the different organs and parts to the total animal structure, the values were greater for the Herefords than for the Holsteins in all except the endocrine gland and visceral fats groups; greater for the Herefords than for the Aberdeen Angus in all except the urogenital, the endocrine gland, and the visceral fats groups; and greater for the Aberdeen Angus than for the Holsteins only in the urogenital and endocrine gland groups. The effect of greater fleshing is clearly shown by these results, for as the total animal structure becomes greater as a result of heavier fleshing, the organs and parts become proportionately smaller. The only group

TABLE 10.—*Degree of difference between breeds for post-mortem items grouped on basis of anatomy and function*

Item	Actual units						Units per 100 pounds of empty body weight					
	Holsteins differ from Herefords		Aberdeen Angus differs from Herefords		Aberdeen Angus differs from Holsteins		Holsteins differ from Herefords		Aberdeen Angus differs from Herefords		Aberdeen Angus differs from Holsteins	
	Items	Average	Items	Average	Items	Average	Items	Average	Items	Average	Items	Average
Plus and minus signs disregarded in determining averages:	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
Body size	27	26.80	3	80.13	3	13.23	26	32.99	2	27.01	2	11.26
Nervous system	1	34.57					1	26.92				
Circulation and respiration	16	55.43	9	39.95	9	17.65	16	26.10	9	37.29	9	33.30
Digestion	13	48.93	13	32.85	13	16.79	13	26.06	13	44.28	13	30.07
Urogenital	4	110.16	4	192.74	4	39.56	4	40.86	4	62.30	4	23.77
Endocrine gland	4	86.24	3	179.49	3	45.20	4	17.84	3	42.89	3	30.62
Visceral fats	2	349.66	2	461.08	2	22.87	2	171.00	2	172.25	2	12.07
All groups combined	67	56.20	34	95.82	34	22.24	66	33.61	33	51.14	33	28.01
Plus and minus signs considered in determining averages:												
Body size	27	+26.09	3	+80.13	3	+13.23	26	−32.86	2	−27.01	2	−11.26
Nervous system	1	+34.57					1	−26.92				
Circulation and respiration	16	+55.43	9	+39.95	9	−17.65	16	−17.62	9	−37.29	9	−33.30
Digestion	13	+47.51	13	+24.21	13	−14.31	13	−18.87	13	−44.28	13	−30.07
Urogenital	4	+65.61	4	+147.57	4	+33.85	4	−6.25	4	+14.98	4	+9.49
Endocrine gland	4	+86.24	3	+179.49	3	+44.74	5	+.63	3	+22.05	3	+18.37
Visceral fats	2	+349.66	2	+461.08	2	+22.87	2	+171.00	2	+172.25	2	−1.17
All groups combined	67	+52.98	34	+87.20	34	+.30	66	−16.45	33	−14.99	33	−18.86

of items which consistently overcame this factor and became greater for Holsteins than for Herefords, and greater for Aberdeen Angus than for either Herefords or Holsteins was the one which included the endocrine glands.

UDDER CHARACTERISTICS AS JUDGED BY ANTE-MORTEM EXAMINATION

Ante-mortem examinations of the udders of the cows used in this study were made in accordance with the general plan adopted by the Bureau of Dairy Industry for studying the udders of the animals in the breeding herd at Beltsville, Md. As explained in a previous publication (*10*), evaluation of the different items that cannot be definitely measured is accomplished by assigning grades ranging from 1 to 9. In each case a grade of 9 indicates the maximum of the characteristic under consideration but does not necessarily signify excellence. In some cases a grade is followed by a plus or a minus sign indicating that the item rates slightly above or below the grade given.

The terms used to describe the udder characteristics compared in this study are defined as follows:

Looseness of udder—the extent to which its covering can be stretched.

Compressibility of udder—the degree to which the udder as a whole responds to pressure.

Abundance of swelling—abundance of congestion resulting from injury, infection, or incidental to parturition.

Abundance of "make-up"—abundance of the substance often present in the udder before parturition and remaining in varying degrees and for varying periods thereafter.

Abundance of gland tissue—quantity of gland tissue in the udder, considering breed and size of animal, stage of lactation, and other factors.

Length of halves—the distance between the anterior and posterior attachments of the gland tissue.

Width of halves—the width of each half above the teats.

Depth of halves—the distance from the abdominal wall to the lowest extremity of the gland tissue.

Nearness to surface—freedom both of deposits of fat around the gland tissue, and of congestion incidental to parturition.

Distinctness of outline—ease with which the outlines and boundaries of the gland tissue can be determined.

Compressibility of gland tissue—the degree to which it responds to pressure.

Mellowness of gland tissue—the degree to which it responds to kneading.

Abundance of fiber—the extent to which the gland tissue is corrugated on the surface, or composed of ropelike strands of tissue.

Coarseness of fiber—the size of the corrugations or strands.

Harshness of fiber—the resistance or harshness of the corrugations or strands.

Stringiness of fiber—the looseness with which the ropelike strands of fiber are held together. In a stringy udder the tissue is compressible and sometimes mellow; in one which is fibrous but not stringy the tissue usually is firm, full, and appears corrugated on the surface.

Openness of cisterns—the size of the openings between the teat canals and the cisterns.

Free space—the distance above the base of the teat which can readily be compressed without marked resistance.

Udder veins—the abundance of veining on the surface of the udder.

Abdominal veins—the abundance of veining on the surface of the abdomen (milk veins).

Milk wells—the size of the openings in the abdominal wall through which the "abdominal" veins pass.

The data representing the different udder characteristics are given in table 11.

TABLE 11.—*Udder characteristics (ante-mortem) of the animals used in the experiment*

Item	Basis of evaluation	Herefords							Holsteins		Aberdeen Angus
		Group 1 (dairy management)				Group 2 (beef management)					
		H-2	H-5	H-6	H-16	H-1	H-4	H-17	No. 299	No. 827	A-300
Looseness of udder	Grade	5	6	6	4	4	4	5	9	6	8
Yieldability of udder	do	7	7	7	7	7	7	6	8	9	7
Abundance of swelling	do	1−	1−	1	1	1−	1	1	1−	1−	------
Abundance of "make-up"	do	1	1	1	1−	1	1−	4	1	1−	------
Abundance of gland tissue	do	1+	2	1	2	2	1−	3	3	2−	5
Length of halves	Inches	6.00	4.50	5.50	8.00	5.00	4.00	9.00	------	------	------
Width of halves:											
Above front teat	do	1.00	1.00	1.00	1.25	1.25	1.00	2.00	------	------	------
Above rear teat	do	1.25	1.00	1.00	1.25	1.25	1.00	2.00	------	------	------
Average	do	1.13	1.00	1.00	1.25	1.25	1.00	2.00	------	------	------
Depth of halves	Grade	2	4	2	4	2	1	3	------	------	------
Nearness to surface	do	5	7	6	5	7	4	4	6	8	4
Distinctness of outline	do	5	7	5	5	7	3	4	7	8	5
Compressibility of gland tissue.	do	5	6	4	6	5	5	4	8	8	4
Mellowness of gland tissue	do	5	6	4	6	5	5	4	8	7	4
Abundance of fiber	do	6	6	5	5	7	5	5	6	6	4
Coarseness of fiber	do	5	6	5	5	6	5	5	4	5	6
Harshness of fiber	do	6	6	5	4	6	6	5	5	5	------
Stringiness of fiber	do	4	4	3	4	4	5	4	4	3	5
Openness of cisterns:											
Left front quarter	do	1	1	1	1	5	1	2	------	3	------
Right front quarter	do	1	1	1	1	5	1	2	------	3	------
Left rear quarter	do	3	1	1	2	1	1	6	------	5	------
Right rear quarter	do	2	1	2	2	2	1	7	------	5−	------
Average	do	1.75	1.00	1.25	1.50	3.25	1.00	4.25	------	4.00	------
Free space:											
Left front quarter	Inches	3.25	3.50	3.50	4.25	3.75	3.25	3.50	4.50	4.75	3.25
Right front quarter	do	3.50	3.50	3.50	4.25	3.75	3.25	3.50	4.50	4.75	3.00
Left rear quarter	do	3.25	3.50	3.25	4.50	3.75	3.25	3.50	4.25	4.75	5.00
Right rear quarter	do	3.00	3.50	3.25	4.25	4.25	3.25	3.50	4.50	4.75	5.00
Average	do	3.25	3.50	3.38	4.31	3.88	3.25	3.50	4.44	4.75	4.06
Udder veins:											
Right	Grade	1	1	1	2	1	2	2	5	3	1−
Left	do	1	1	1	2	1	2	2	4	2	1−
Abdominal veins:											
Right	do	1	2	2	3	3	3	4	6	5	1−
Left	do	3	3	1	2	3	3	4	7	7−	1−
Milk wells:											
Right	do	1	2	1	2	2	1	2	7	3−	1
Left	do	2	3	1−	2	1	1	2	7	3	6

The estimates on the various udder characteristics, as given in table 11, were made on all the animals while they were dry and shortly before they were slaughtered. The length of time the individual animals had been dry varied greatly.

In the estimates of those udder characteristics that are associated with "quality of udder" (i. e., looseness of udder, yieldability of udder, compressibility of gland tissue, mellowness of gland tissue, stringiness of fiber, and free space), there was no great difference between the two groups of Herefords. The two Holstein cows averaged considerably higher than the Herefords for most of these items, although for some items individual Herefords were graded as high as the Holsteins. The Aberdeen Angus cow was close to the average of the Herefords for

most of these items. For looseness of udder and stringiness of fiber, however, she was given a higher rating than the Holsteins.

In those characteristics that might be termed antagonistic to quality of udder (such as abundance, coarseness, and harshness of fiber) there was no great difference on the average between the grades for the two groups of Herefords, the Holsteins, and the Aberdeen Angus.

The greatest and most consistent differences between the Holsteins and the Herefords and the Aberdeen Angus were in the abdominal veins, milk wells, and udder veins, for which the Holsteins were definitely superior. This may be to some extent indicative of the greater blood flow from the udder.

Although the grades for quality of udder are shown to be greater for the Holsteins than for the Herefords or the Aberdeen Angus, the differences do not approach the great difference in producing capacity that actually existed between the Holsteins and the Herefords, and that presumably also existed between the Holsteins and the Aberdeen Angus.

POST-MORTEM STUDIES OF THE UDDER

SIZE AND CAPACITY

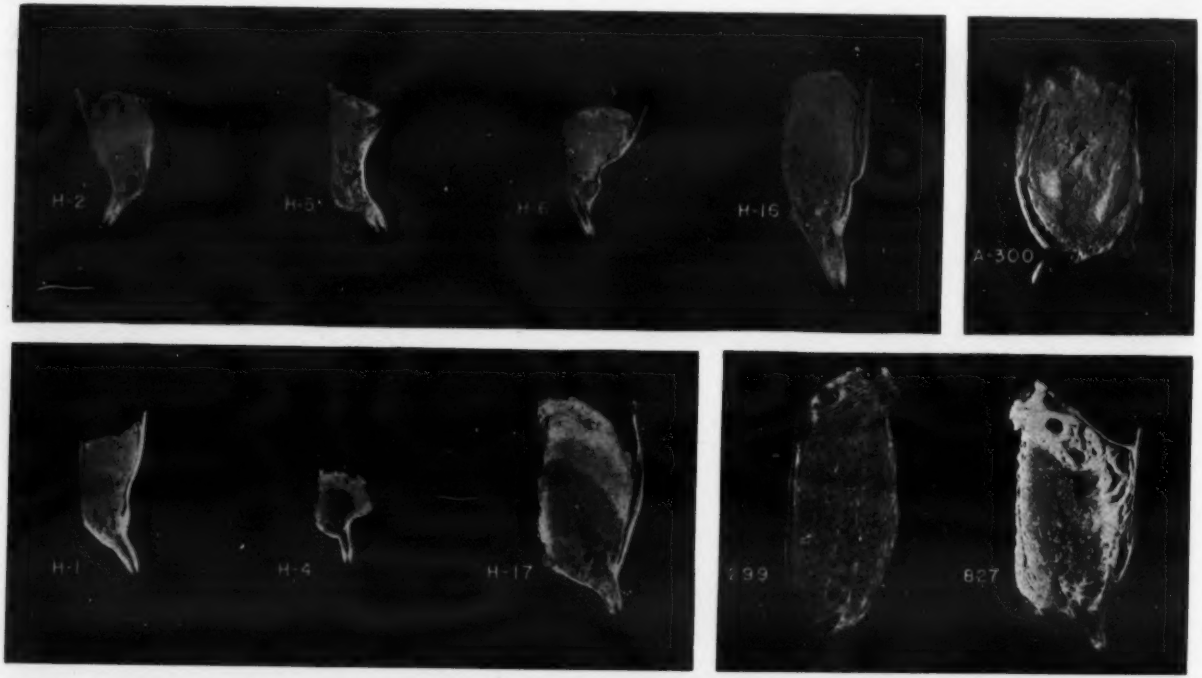
The method of studying the udder after its amputation was described in considerable detail in a previous publication (*10*). Size of udder refers to its empty weight. Capacity of udder is the quantity of formalin held by the secretory system of the udder expressed in terms of equivalent weight of milk. The relation of capacity to weight of udder, expressed as a percentage, is obtained by dividing the capacity by the empty weight and multiplying the result by 100. It is a measure of the fluid-holding capacity of the secretory system per unit of udder weight. Data for size, capacity, and relation of capacity to weight, for the Herefords, the Holsteins, and the Aberdeen Angus are given in table 12.

In empty weight of udder the two groups of Herefords differed but slightly, group 2 being only 2.30 percent greater than group 1; the Holsteins averaged 160.16 percent greater than the Herefords; the Aberdeen Angus was 336.08 percent greater than the Herefords and 67.62 percent greater than the Holsteins.

In capacity of udder the Herefords in group 2 averaged 53.32 percent greater than those in group 1; the Holsteins averaged 520.33 percent greater than all the Herefords; and 359.78 percent greater than the Aberdeen Angus; the Aberdeen Angus averaged 34.92 percent greater than the Herefords.

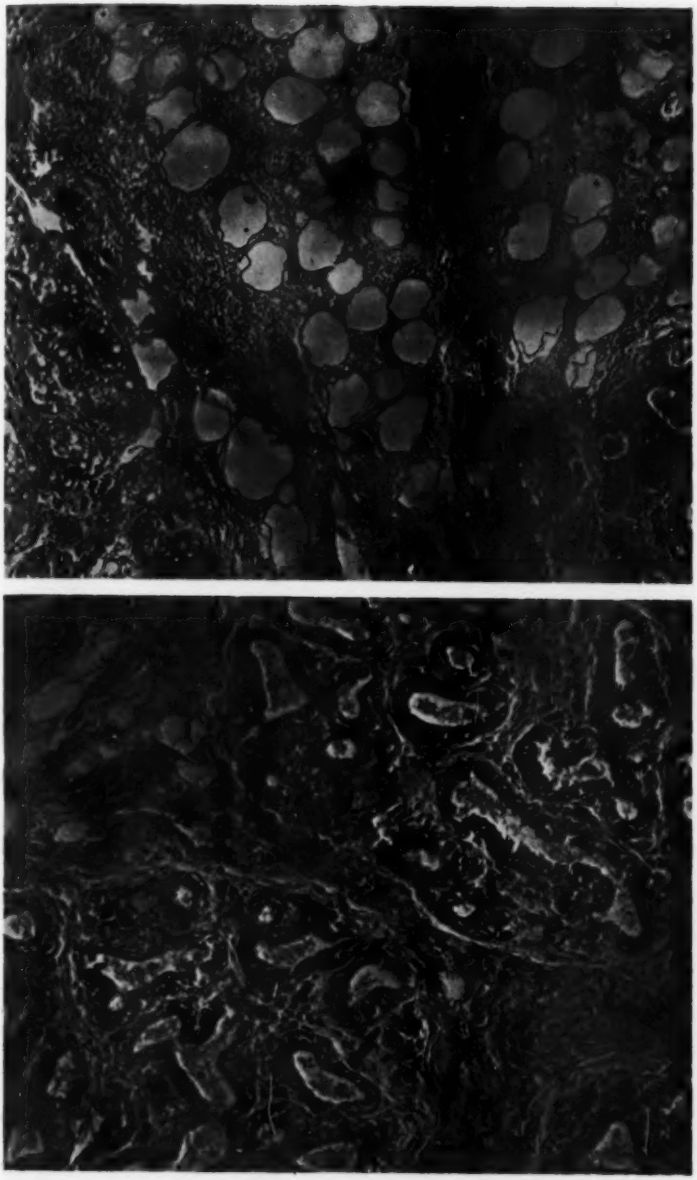
For the values representing the relation of capacity to weight of udder, the Herefords in group 2 averaged 74.86 percent higher than those in group 1; the Holsteins average 130.12 percent higher than the Herefords; the Aberdeen Angus was 69.96 percent lower than the Herefords, and 86.95 percent lower than the Holsteins.

It has been found (*4, Rept. 1932, p. 7*) that the capacity of lactating udders is considerably greater than that of nonlactating udders. All the cows in this study were nonlactating, but the period of time since being dried off varied to some extent. It is not at all unlikely that the prolonged inactivity of the Aberdeen Angus may have resulted in a greater deposition of fat around the gland, which would reduce the value for relation of capacity to weight of udder even though the capacity itself might not have been greatly affected. It might appear



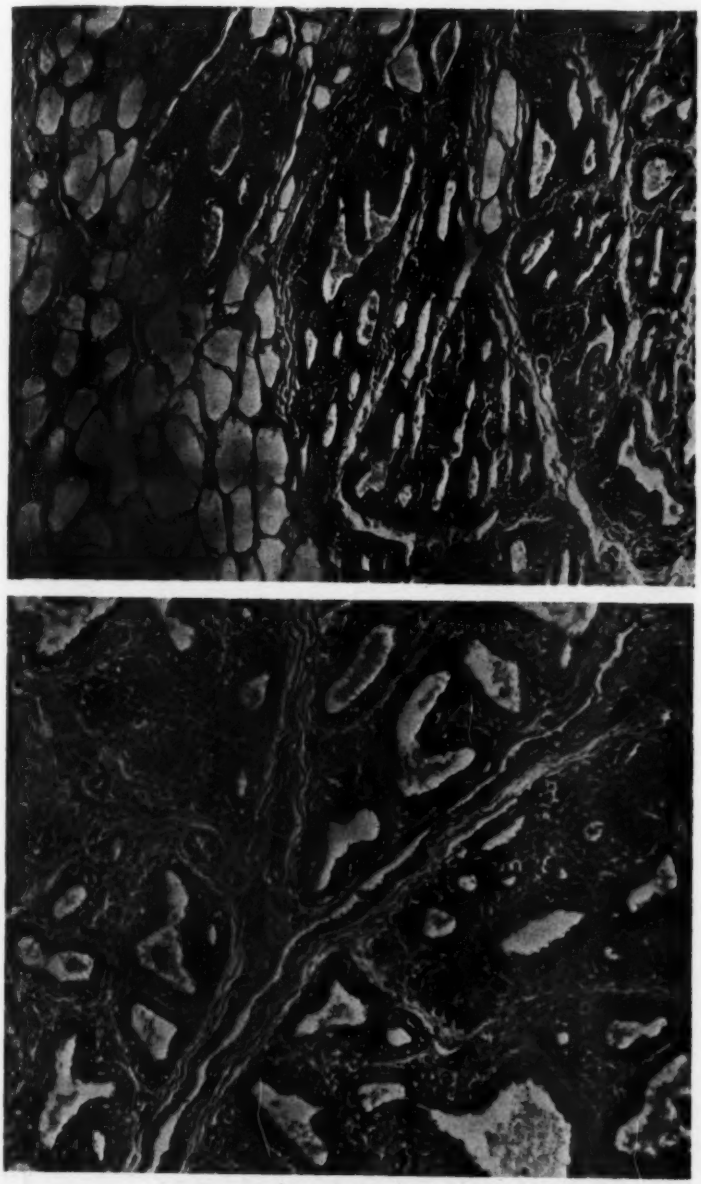
Vertical transverse sections through rear quarter of each of the 10 udders studied, reduced to same scale to show comparative size. In some a large proportion of the area consists of body fat rather than glandular tissue.

Vertical transverse section through a rear quarter of the udder of H-2.



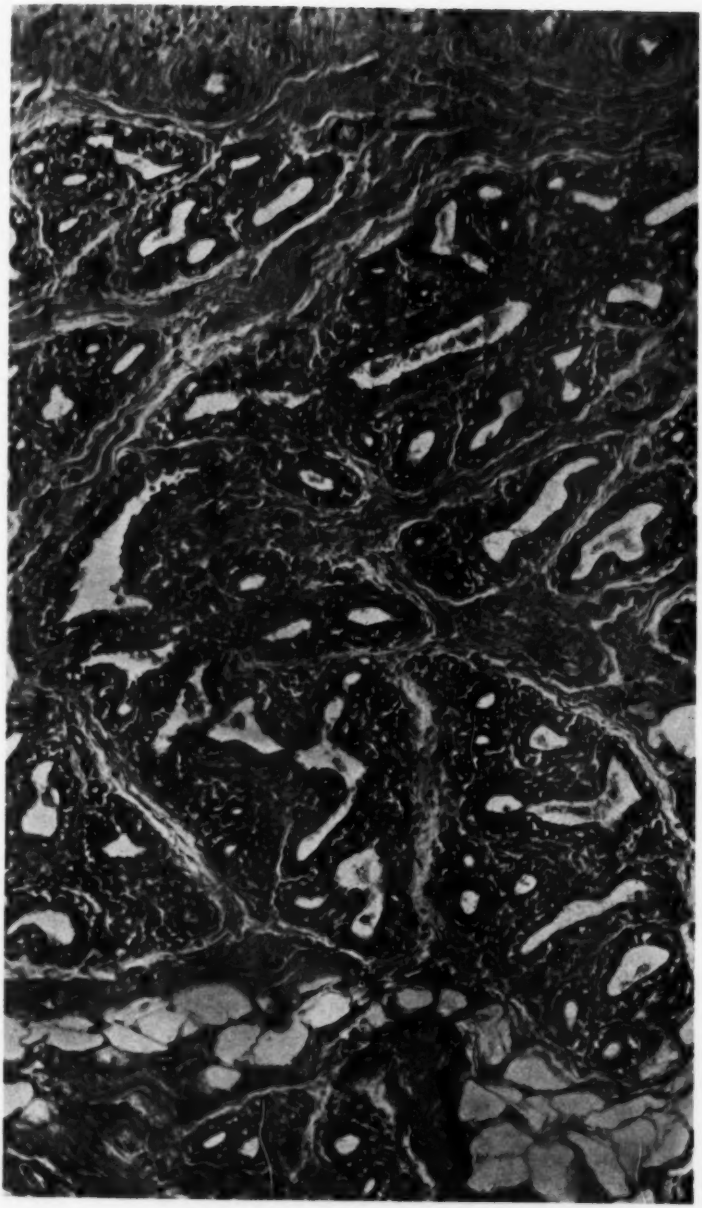
Photomicrographs of tissue from the udder of H-2.

Vertical transverse section through a rear quarter of the udder of H–5.



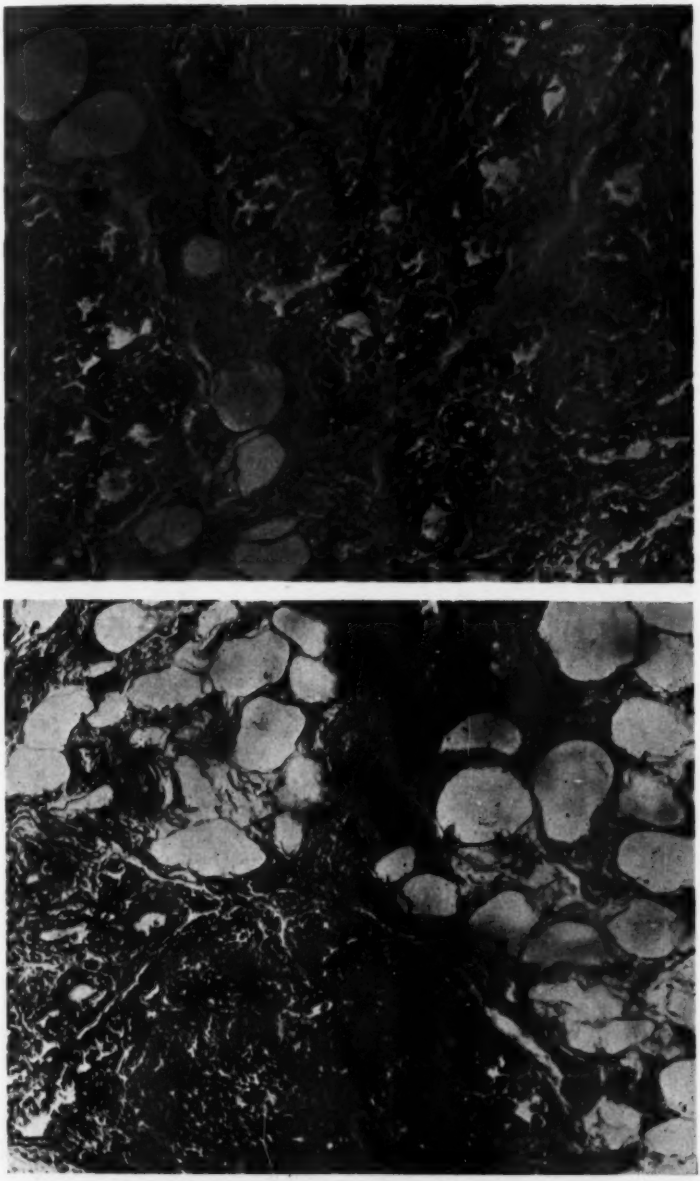
Photomicrographs of tissue from the udder of H-5.

Vertical transverse section through a rear quarter of the udder of H-6.



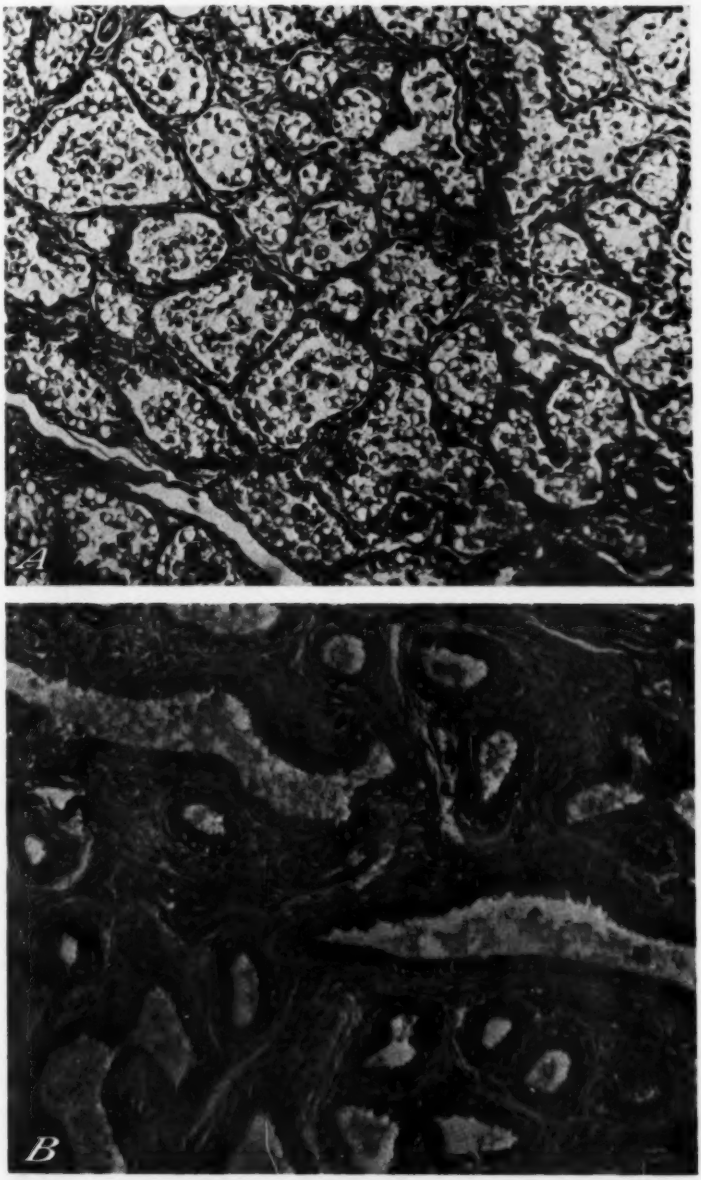
Photomicrograph of tissue from the udder of H-6.

Vertical transverse section of a rear quarter of the udder of H-16.



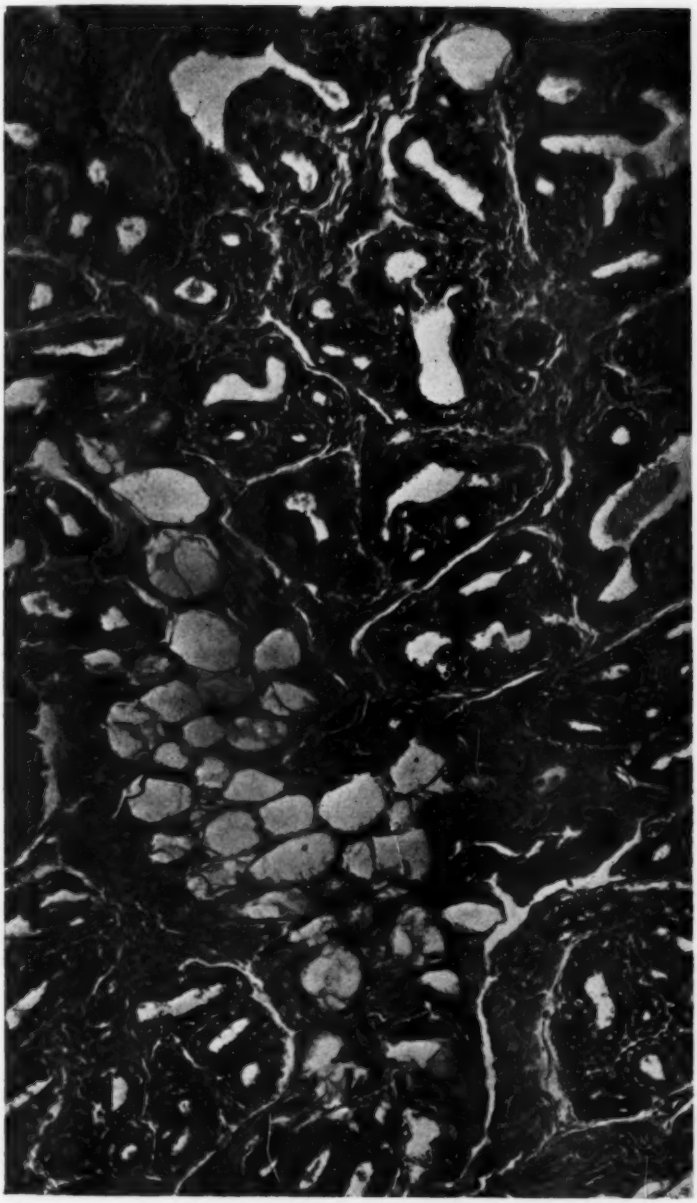
Photomicrographs of tissue from the udder of H–16.

Vertical transverse section through a rear quarter of the udder of H-1.



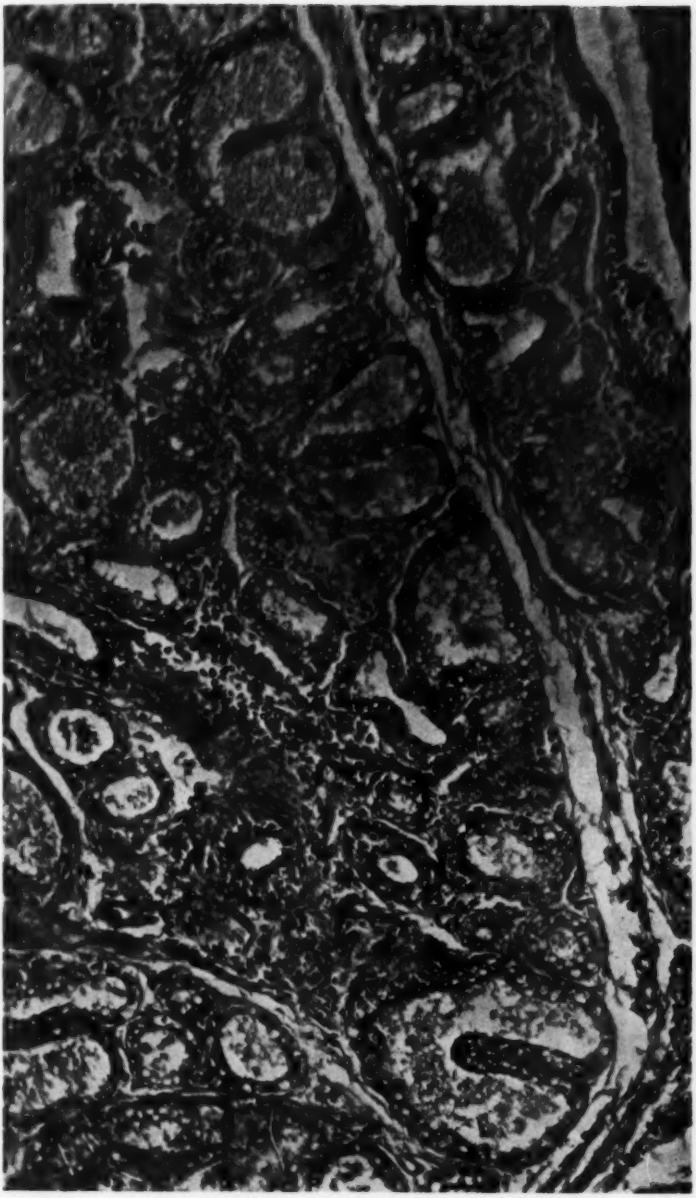
Photomicrographs of tissue from the udder of H–1: *A*, Functioning tissue from the upper portion of the front quarter; *B*, nonfunctioning tissue from the lower portion of the rear quarter.

Vertical transverse section through a rear quarter of the udder of H–4.



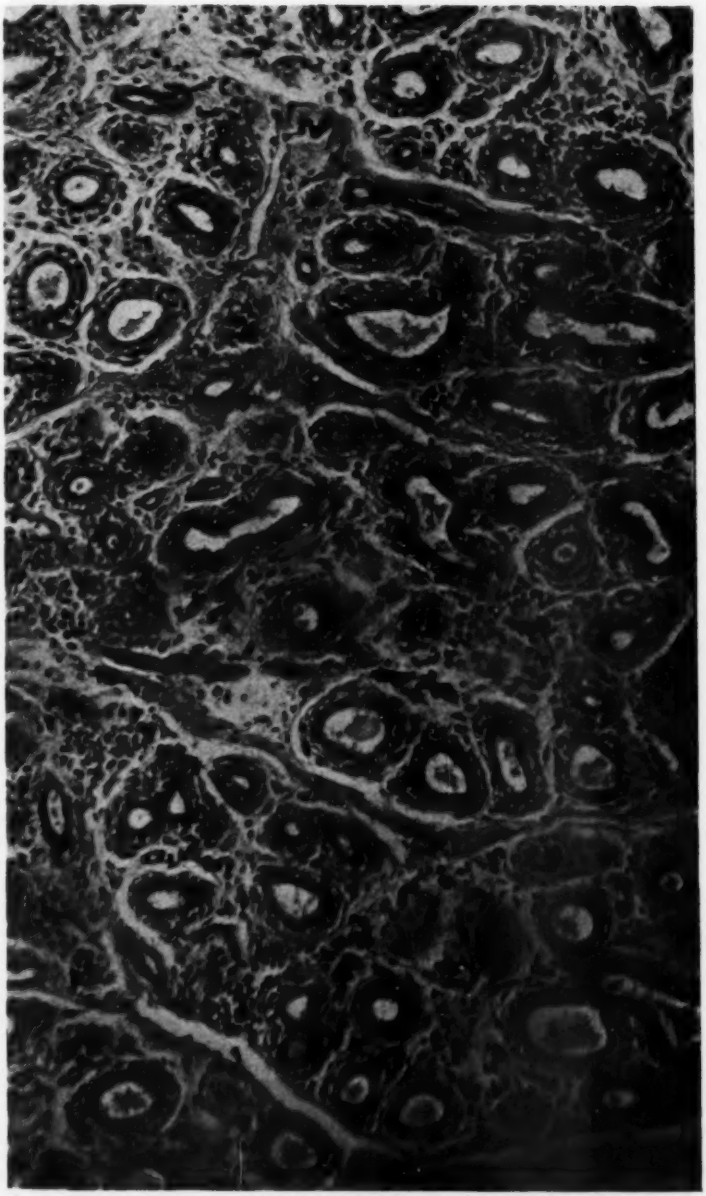
Photomicrograph of tissue from the udder of H-4.

Vertical transverse section through a rear quarter of the udder of H-17.

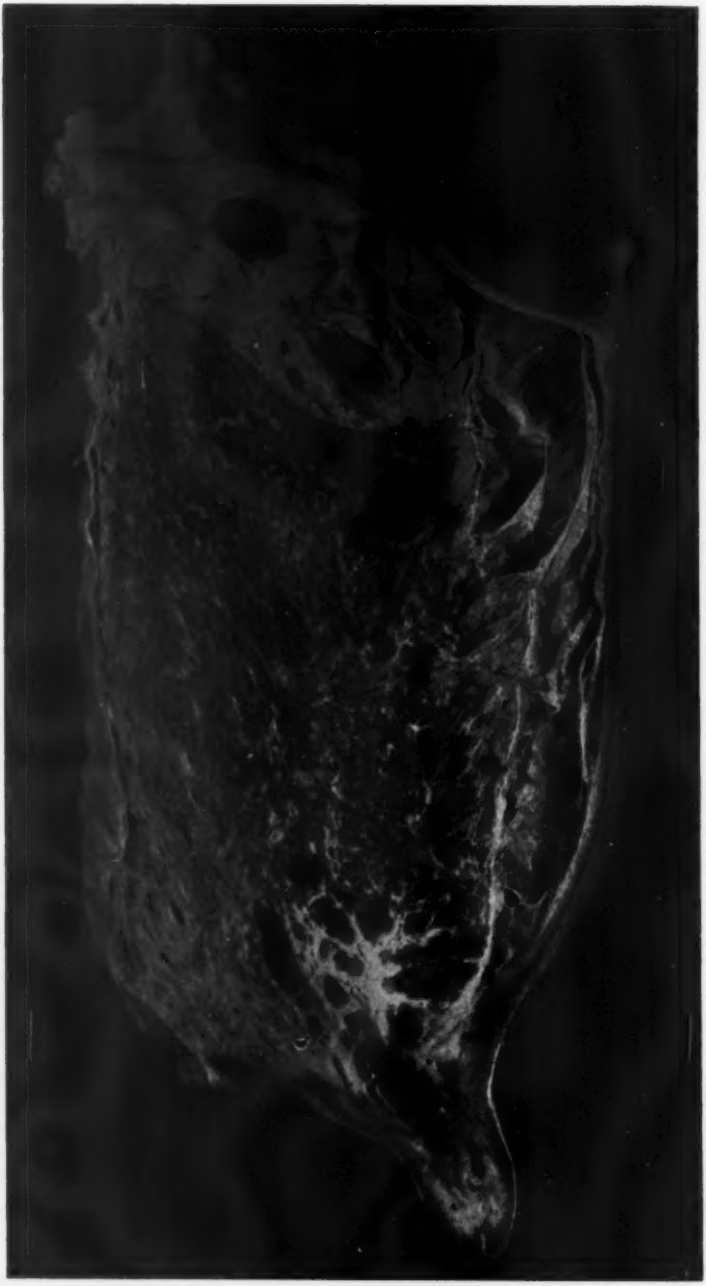


Photomicrograph of tissue from the udder of H–17.

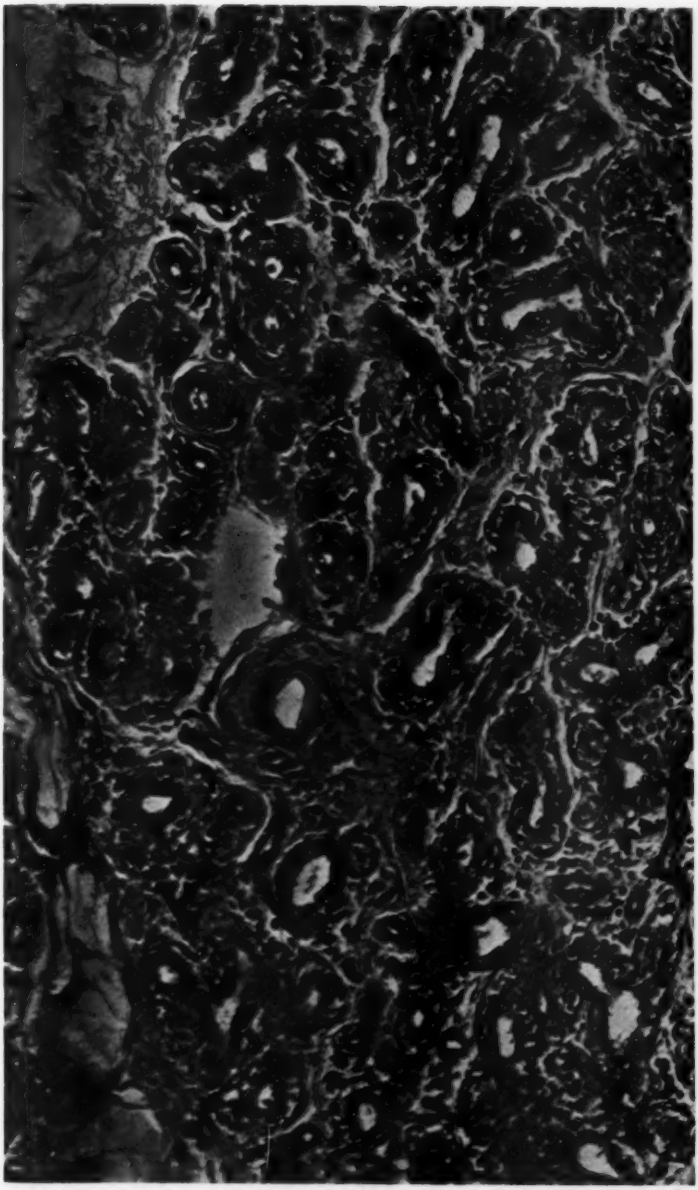
Vertical transverse section through a rear quarter of the udder of Holstein cow no. 290.



Photomicrograph of tissue from the udder of Holstein cow no. 299.

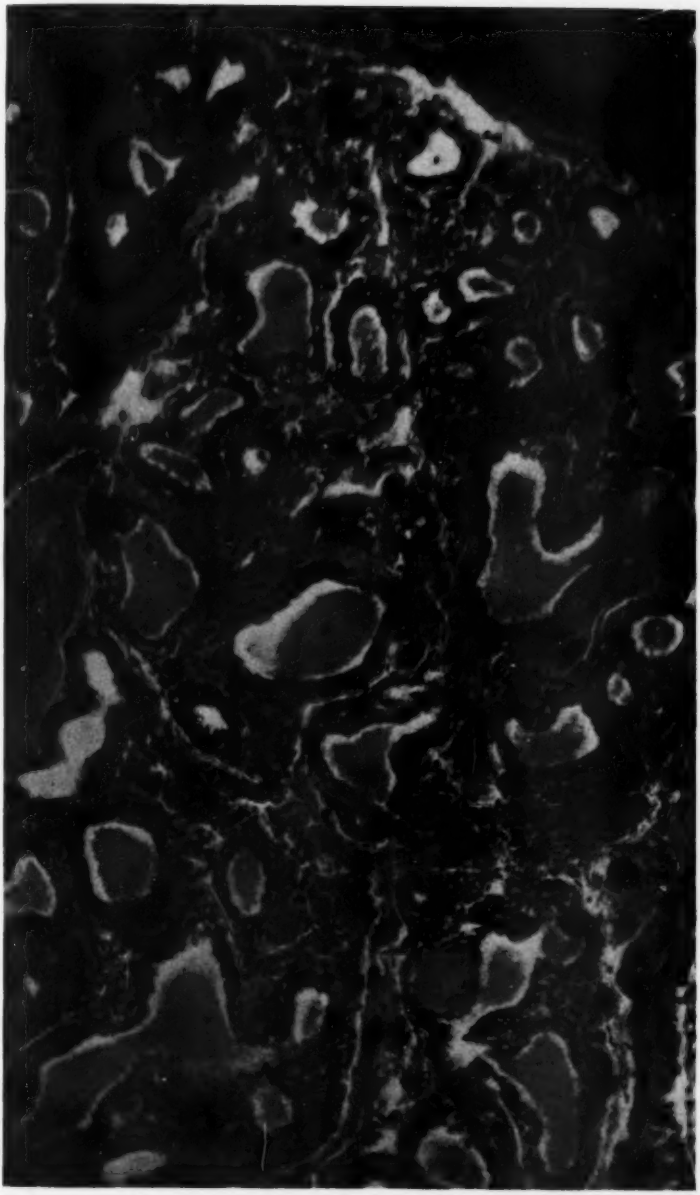


Vertical transverse section through a rear quarter of the udder of Holstein cow no. 827.



Photomicrograph of tissue from the udder of Holstein cow no. 827.

Vertical transverse section through a rear quarter of the udder of Aberdeen Angus cow A-300.



Photomicrograph of tissue from the udder of Aberdeen Angus cow A-300.

TABLE 12.—*Size and capacity of udder of Herefords, Holsteins, and Aberdeen Angus*

Item	Herefords										Holsteins			Aberdeen Angus
	Group 1 (dairy management)					Group 2 (beef management)				Average for both groups				
	H-2	H-5	H-6	H-16	Average	H-1	H-4	H-17	Average		No. 299	No. 827	Average	A-300
Size (empty weight) of udder...pounds..	9.95	7.15	8.35	14.50	9.99	6.30	6.35	18.00	10.22	10.09	30.50	22.00	26.25	44.00
Quantity of fluid held by 2 right quarters of udder.....cubic centimeters..	500	700	945	2,225	1,092.50	2,080	490	2,460	1,676.67	1,342.86	9,980	6,669	8,324.50	1,810
Milk equivalent capacity of secretory system of entire udder.....pounds..	2.27	3.18	4.30	10.11	4.97	9.45	2.23	11.18	7.62	6.10	45.36	30.31	37.84	8.23
Relation of capacity to weight of udder percent..	22.81	44.48	51.50	69.72	47.13	150.00	35.12	62.11	82.41	62.25	148.72	137.77	143.25	18.70
Stage of dryness:														
Time since last milked, months-days	3-12	1-9	3-14	0-26	.....	0-18	.....	.....	.....	.....	0-22	7-12	.....	(1)

[1] About 25 months.

12368—37——3

at first that the comparatively high value for relation of capacity to weight of udder in the case of H–1 was to some extent the result of having nursed a calf until a short time before she was slaughtered. However, among the other Herefords the duration of the dry period did not differ greatly, and was nearly the same for H–5, H–16, and H–1, yet the capacity and relation of capacity to weight of udder for these three animals differed greatly. The dry periods of the Holsteins also varied from 22 days to more than 7 months, but their ratios of capacity to weight of udder were similar. Apparently variations in the duration of gland inactivity are at least only partly responsible for the differences in udder capacity or for the relation of capacity to weight of udder shown in this study, unless it be in the case of the Aberdeen Angus.

The fluid-holding capacity of the udder per unit of weight is consistently low for the beef cows studied, indicating that these udders contain a low quantity of secreting tissue in proportion to fat or connective tissue.

The number of animals is not sufficiently large to warrant the calculation of correlation coefficients but there appears to be a high positive relationship between empty weight, capacity, and ratio of capacity to weight of udder and milk production, except where the differences in production are so small as to be of no importance. In other words, there is a high positive correlation if the Holsteins, the highest producing Hereford, and the three lowest producing Herefords are considered as separate groups, but little if any correlation among the three lowest producing individual Herefords.

In view of the fact that the Holsteins produced 2,461 percent more milk and 1,681 percent more butterfat than the Herefords in group 1, the 163 percent greater empty weight of the Holstein udders, the 661 percent greater capacity of their udders, and the 204 percent greater capacity to weight ratio of their udders seem relatively small differences. These differences in udder size and capacity, however, were much more significant of the difference in producing capacity between the breeds than any of the udder characteristics studied on the live animals. This is in accordance with the results obtained in the study (*10*) of quality, size, capacity, gross anatomy, and histology of cow udders in relation to milk production in 11 registered and grade cows of dairy breeds, which showed that the only significant correlations between udder characteristics and producing capacity were for size and capacity of udder.

GROSS ANATOMY

The method of preparing and sectioning udders in making a comparative study of their gross anatomy was described in a previous publication (*4, Rept. 1929, p. 8*). In each case the right half of the udder was used in measuring capacity, and subsequently frozen, sectioned, and photographed. The left half was used for histological studies. The comparative size of the 10 udders used in this study is illustrated in plate 1, which shows a vertical transverse section through a rear quarter of each udder, all reduced to the same scale. Plates 2, 4, 6, 8, 10, 12, 14, 16, 18, and 20 show in greater detail the appearance of the gross anatomy of a vertical transverse section through a rear quarter, for the seven Herefords, the two Holsteins, and the Aberdeen Angus. A brief description of the gross anatomy is given under a

general discussion of the performance and udder characteristics of each cow.

HISTOLOGY [5]

The comparative histology of the tissues from the udders of the cows was studied according to the method described in a previous publication (*10*). The results obtained are reported as a part of the general discussion of the performance and udder characteristics of the individual cows. The histological appearance of the tissue from each udder is shown in plates 3, 5, 7, 9, 11, 13, 15, 17, 19, and 21.

UDDER CHARACTERISTICS AND PERFORMANCE OF EACH COW

HEREFORD COW H–2

Hereford cow H–2 was kept in the dairy herd and milked twice daily through one lactation period. Her total production for the entire lactation period of 153 days was only 126.00 pounds of milk and 6.52 pounds of butterfat. She had been dry for 3 months 12 days and pregnant for 157 days when slaughtered. The fetus weighed 3,561 grams (7.85 pounds). Ante-mortem examination showed that her udder, though extremely retarded in development and lacking in gland tissue, was of fair quality, and was more than medium in abundance of fiber; the openings from the teat canal to the cisterns were on the average very small and the free space was comparatively low. The udder was relatively low in weight, next to the lowest in capacity, and next to the lowest in relation of capacity to weight of udder.

Gross anatomy (pl. 2).—The gland tissue was very scanty, and limited to only a small proportion of the area of the sections. The sections through or close to the teats appeared to contain about one-third gland tissue; those near the front and rear of the udder contained little or none. The greater part of every section consisted of what appeared to be fat. The gland tissue was comparatively open in structure with a small but well circumscribed cistern. The openings to the cisterns were comparatively small. The ducts were well distributed and of medium size. Very little visible connective tissue was observed. The gland tissue was of medium firmness and the fat was very firm.

Histology.—Because of the extremely fatty condition of this udder, sections for histological study could be obtained only from areas in the lower portions of the front and rear quarters. This gland was found to be in the complete resting state with the exception of a few lobules here and there which showed some activity. This udder showed a rather heavy fibrous framework, and interlobular fat deposits were noted in the different areas examined. The areas illustrated in plate 3 were taken from a point near the base of the left rear quarter.

General.—There is no record of this cow having had any udder disturbance requiring treatment. The ante-mortem observations relative to abundance of fiber or connective tissue are supported by the histological findings, though the connective tissue is not readily visible in the gross sections. Liberal production could not be expected from an udder having the limited quantity of gland tissue indicated by the section illustrated.

[5] The histological studies were made by G. T. Creech, Pathological Division, Bureau of Animal Industry, U. S. Department of Agriculture.

HEREFORD COW H–5

Hereford cow H–5 was kept in the dairy herd and milked twice daily through a lactation period which continued for 202 days and yielded a total of 255.4 pounds of milk and 9.86 pounds of butterfat. She had been dry for 1 month 9 days and pregnant for 73 days when slaughtered. The fetus weighed 46 grams. Her udder was above the average in quality, yet extremely retarded in development and deficient in quantity of gland tissue. Ante-mortem examination indicated more than an average quantity of fiber, extremely small openings to the cisterns, and comparatively low free space. This udder was third from the lowest in empty weight and in capacity, and fourth from the lowest in relation of capacity to weight.

Gross anatomy (pl. 4).—Though the udder was very small, it consisted almost entirely of gland tissue with only small areas of fat in any of the sections except those at the extreme rear. In the rear quarter, especially in the lower half, the tissue was distinctly porous, and the cistern was of good size and somewhat divided. In the front quarter the cistern was not distinctly circumscribed but consisted of a honeycomb mass of ducts covering a relatively large part of the area above the teat. The opening between the teat and the cistern was of good size in the rear quarter and even larger in the front quarter. The amount of visible connective tissue was not great and it was comparatively finely divided. Both the gland tissue and the fat were firm at the time the sections were photographed.

Histology.—The histological examination showed this udder to be in the resting state. Sections were obtained from only three locations. Areas of round cell infiltration were noted in this gland, and in certain areas there appeared to be some increase in the interlobular and intralobular connective tissue. Large areas of fat as well as smaller interlobular fat deposits were observed in this udder. The areas illustrated in plate 5 were taken from a point in the upper portion of the left rear quarter.

General.—There is no record of this cow having had any udder disturbances requiring treatment. The ante-mortem observations indicated a greater quantity of fiber than was observed in the gross anatomy sections. Though excessive fat deposition was not indicated by ante-mortem examination or by the gross sections the histological studies indicated that considerable deposition had taken place. Though the proportion of gland tissue to fat was high, the quantity of gland tissue was so small that liberal production of milk could hardly have been possible.

HEREFORD COW H–6

Hereford cow H–6 was kept in the dairy herd and milked twice daily through a lactation period which, with much difficulty, was kept active for 159 days, and which resulted in a total yield of only 80.6 pounds of milk and 3.73 pounds of butterfat—an average daily milk production of 0.51 pound. This is the poorest production for any cow in this group. She had been dry for 3 months 14 days and pregnant for 91 days when slaughtered. The fetus weighed 192 grams. The udder was one of the lowest in quality in this group. It was extremely retarded in development, and very deficient in quantity of gland tissue. The fiber was of average abundance, the openings to cisterns were very small, and the free space was comparatively low

The udder was fourth from the lowest in empty weight and in capacity, and fifth from the lowest in relation of capacity to weight.

Gross anatomy (pl. 6).—The gland tissue in this udder could not readily be distinguished from the fat. There was a layer of firm fat across the upper surface, but the rest was soft and lacking in outline pattern and color differentiation. Incomplete freezing of the udder when sectioned may have resulted in a tendency for the saw to tear the tissue, leaving the surface rough, but it could not have been entirely responsible for the lack of differentiation in color in the gross sections of this udder. Apparently the gland tissue was limited in quantity and interspersed with fat. The cisterns in both front and rear quarters were small, round, and tubular, and little more than continuations of the teat canal, though the cistern in the rear quarter was somewhat divided at its upper extremity. The openings from the teat canal to the cistern in both front and rear quarters were much larger than the ante-mortem grades would indicate. Aside from a small area in the immediate vicinity of the cisterns, the tissue was dense and almost devoid of visible ducts. An unusally large quantity of visible connective tissue was present, although only an average quantity was indicated by the ante-mortem examination.

Histology.—This udder was small and very fat; consequently sections were obtained only from areas in the lower part of the front and rear quarters. This gland was in the resting state and showed little deviation from the normal, other than the large amount of fat which appeared, not only as interlobular deposits, but as rather large areas of fat here and there, in places ordinarily occupied by normal gland tissue. The area illustrated in plate 7 was taken from near the center of the left front quarter.

General.—Both the gross anatomical and histological studies indicate a marked lack of secretory tissue and an excess of fat, though the fatty condition was not noted at the time of ante-mortem examination. As shown in table 4, this cow was milked until she was producing an average of only 0.17 pound of milk daily. The average production for the first 10 days in milk was only 1.34 pounds, and the highest for any one day in the lactation period was only 2.4 pounds. Again it appears that failure to function was due to extreme deficiency in secretory tissue in the udder.

HEREFORD COW H–16

Hereford cow H–16 was kept in the dairy herd and milked twice daily through a lactation period which continued for 329 days and yielded 1,767.8 pounds of milk and 90.52 pounds of butterfat. Her production and persistency were far superior to those of any of the other Herefords for which production records were obtained. She had been dry for 26 days and pregnant for 223 days when slaughtered. The fetus weighed 17,464 grams (38.5 pounds). Ante-mortem examination showed that her udder was near the average for the group in quality, the fiber was of medium abundance, the openings to the cisterns were very small, and the free space was high. Though this udder was small and very deficient in gland tissue when compared with those of dairy cows, it exceeded in dimensions that of any other Hereford in the dairy herd. The empty weight of udder was higher than that of the other Herefords having production records, but ranked fifth from the highest in the entire group of cows compared in this

study. The udder was fourth from the highest in the entire group in capacity, and in relation of capacity to weight of udder.

Gross anatomy (pl. 8).—Though the quantity of gland tissue was greater than that of any of the other Herefords in the dairy herd, it occupied only about one-half to two-thirds of the area of sections through the teats and very little or none in sections from other parts of the udder. The outline of the gland tissue, however, was distinct and readily distinguishable from the areas of fat above and around it. The cistern in the rear quarter was small, divided, and appeared to be a continuation of the teat canal; the one in the front quarter was similar except that it was more tubular and less divided. The tissue was fairly firm and inclined to be dense except in areas close to the cisterns. The sections contained comparatively large quantities of visible connective tissue which was uniformly distributed, although the ante-mortem examination indicated only an average quantity of fiber. The areas of fat were of moderate firmness. The openings from the teat canals to the cisterns were considerably larger than the ante-mortem grades would indicate, and the cisterns were smaller than the grades for free space would suggest.

Histology.—This was a small, fatty udder. Owing to the large amount of fat present it was possible to section only an area from the lower portion of the rear quarter for histological study. The gland was found to be in the resting state. There was a limited amount of round cell and leucocytic infiltration. The areas sectioned and illustrated in plate 9 showed a considerable amount of fat, both interlobular and in areas ordinarily occupied by gland lobules, and were taken from a point near the base of the left rear quarter.

General.—This cow was somewhat older, larger, and better developed than the others already discussed. Although her udder was described as small and deficient in gland tissue, its development and its capacity for production were superior to those of the other three Herefords kept in the dairy herd.

HEREFORD COW H–1

Hereford cow H–1 was kept in the beef herd and allowed to nurse her calf from December 14, 1928, until late in May 1929. She was not pregnant when slaughtered. Though the udder was very small and very deficient in glandular development it was about medium in quality. According to ante-mortem observations the fiber was abundant, and above medium in coarseness and harshness; the openings from teat canal to cisterns were variable, being graded as medium in the right front and very small in the right rear quarter; and the free space was about average. In empty weight this udder was the smallest in the entire group, in capacity it was fifth from the highest, and in relation of capacity to weight of udder it was higher than for any other cow in any of the breeds compared in this study.

Gross anatomy (pl. 10).—Though the udder was the smallest in the group it was made up almost entirely of gland tissue. There were practically no visible areas of fat in any of the sections except those at the extreme rear of the udder. This is in agreement with the high grade for "nearness to surface" (table 11). The udder was not completely frozen when sectioned, but the cuts were fairly clean and the surfaces of the sections were smooth. In the front quarter the cistern was of medium size, definitely circumscribed, and the opening into it

from the teat canal was large. In the rear quarter the cistern was very small, somewhat divided, and the opening into it was much smaller than in the front quarter. The size of openings into cisterns corresponds rather well with the grades assigned on ante-mortem examination, though the grades for free space do not appear to be related closely to the size of the cisterns. Only a moderate amount of connective tissue was visible in the gross sections although the ante-mortem examination indicated an abundance of fiber. The tissue was comparatively dense, the ducts being limited almost entirely to areas close to the cisterns and to the lower half of each section. The tissue was described as a trifle soft but more like the secretory tissue of a dairy cow than that of any of the other Herefords.

Histology.—One of the sections, from the lower portion of the rear quarter (pl. 11, *B*), showed this particular area of the gland to be in a complete resting state. Sections from other areas (pl. 11, *A*) showed evidence of considerable glandular activity. Many of the alveoli were filled with free cells containing fat droplets, giving the various lobules as a whole a peculiar fatty appearance in some sections. Interlobular fat deposits were seen in some of the sections.

General.—The gross sections consisted almost entirely of gland tissue, although the actual quantity was very small. The shortness of the dry period preceding slaughter may have been partly responsible for the close resemblance of the tissue in this udder to that of a dairy cow. Moreover, this cow was in a poor condition of flesh, which may have affected the amount of deposition of fat in the udder.

HEREFORD COW H-4

Hereford cow H–4 was kept in the beef herd. She aborted December 20, 1928; and information is not available as to whether she was nursed by the calves of other cows, or the possible effect of such nursing on the length of the lactation period and the condition of the mammary gland. She was pregnant when slaughtered, but the date of breeding was not known. The fetus weighed 236 grams. The udder appeared on ante-mortem examination to be the smallest in the entire group, and its empty weight was within 0.05 pound of the lowest recorded. The glandular development was extremely deficient, the quantity and proportions closely approximating those of a 6-month-old Holstein calf. The udder quality was far below the average for the group of udders compared in this study. The fiber was of medium abundance and coarseness. The openings from the teat canals to cisterns appeared on ante-mortem examination to be extremely small and the free space was one of the two lowest in the group. This udder was not only next to the lowest in empty weight, but it was the lowest of all in capacity, and third from the lowest in relation of capacity to weight.

Gross anatomy (pl. 12).—Not only was the udder extremely small, but it contained a comparatively large proportion of fat, thereby supporting the grade assigned for "nearness to surface" (table 11). The gland tissue did not occupy more than two-thirds of the area of any section, and in most sections it did not occupy more than one-half of the area. In the rear quarter the cistern was very small and the opening from the teat canal was extremely small. In the front quarter also the cistern was very small, but the opening from the teat canal was very slightly larger than in the rear. These findings are

generally in accord with ante-mortem observations on size of openings and amount of free space. The gland tissue was not definite in outline and not easily distinguishable from the fat. Except for a small area close to the cistern the ducts were small and very few in number. It appeared that a fairly large quantity of connective tissue was present in this udder and that the gland tissue was interspersed with fat. The gland tissue was inclined to be soft, but the surrounding fatty areas were very firm.

Histology.—This udder was very small and extremely fat, and sections could be obtained only from areas near the center of the front quarters and the lower part of the rear quarter. This gland was in the resting state and showed little evidence of functional activity. The outstanding histological finding in this udder was the excessive amount of fat present and intermixed with the glandular tissue. There were not only extensive interlobular fat deposits, but in places there were areas the size of several lobules occupied by fat, instead of the normal gland tissue. The area illustrated in plate 13 was taken from near the center of the left front quarter.

General.—This udder probably had the least grandular development of any compared in this study, though in some respects that of H–2 was not greatly different. The gross anatomical findings support the ante-mortem observations unusually well for abundance of gland tissue and its closeness to the surface, abundance of fiber, and size of cistern openings. Uncertainty as to the duration of lactation and the possible effect of abortion on mammary activity and development make conclusions difficult. It appears, however, that this cow did not possess the necessary development for liberal lactation.

HEREFORD COW H–17

Hereford cow H–17 was kept in the beef herd following an abortion on June 12, 1928. As in the case of H–1, information is lacking as to her lactating capacity and as to whether she was nursed by the calves of other cows. Moreover she was in advanced pregnancy (271 days) when slaughtered and her udder was "making up" and therefore not comparable to the others in regard to many characteristics. The fetus weighed 27,443 grams (60.5 pounds). Though small and deficient in gland tissue in comparison with that of a dairy cow, the udder appeared to be superior to that of any of the other Herefords at the time the ante-mortem observations were made. In quality, however, it was well below the average for the group of cows compared. The fiber was of medium abundance, coarseness, and harshness. The openings from the teat canals to the cisterns appeared on ante-mortem examination to be larger on an average than for any other cow in the group, the right front one being very small but the right rear one large. The amount of free space appeared to be slightly below medium. In empty weight the udder ranked fourth from the highest, in capacity it was third from the highest, and in relation of capacity to weight it was fifth from the highest.

Gross anatomy (pl. 14).—Though this udder was of fairly good size, a large proportion of the area of the sections consisted of fat. In the sections carrying the teats only about 50 to 60 percent of the total area consisted of gland tissue; in the sections near the front and rear of the udder there was little or no gland tissue. The outline of the gland tissue was fairly distinct, though in many sections there was an

area surrounding it which seemed to contain a large proportion of connective tissue and to be intermediate between the gland tissue and the fat. The udder was not well frozen when sectioned, but the surfaces of the sections were fairly smooth. In the rear quarter the cistern was of moderate size but the front cistern was large. Both cisterns were divided. Though the ante-mortem examination indicated a rather marked difference between the front and rear quarters in size of opening from teat canal to cistern, the gross sections showed that both were comparatively large. The tissue was of more than average openness, especially in the vicinity of the cisterns. A medium quantity of connective tissue was visible in the sections though it was rather indistinct in outline. The tissue itself was described as mushy but the areas of fat were of medium firmness.

Histology.—This udder showed glandular activity in all the areas examined, with indications here and there of the gland being partly in the resting state. A few small areas of round cell infiltration were noted, but for the most part this gland was normal in appearance. The fibrous connective tissue of this udder had the appearance of being of a soft or loose texture. The area illustrated in plate 15 was taken from the upper portion of the left front quarter.

General.—The ante-mortem observations are usually well supported by the gross-anatomical findings for most of the items compared. The quantity of gland tissue appeared to be nearly the same as for H–16, the Hereford kept in the dairy herd, which closely approximated H–17 in age and in size. It would appear that the advanced stage of gestation was largely responsible for the indications of activity reported in the histological study, and to some extent for the size of the udder and the quantity of gland tissue present.

HOLSTEIN COW NO. 299

Cow 299, a registered Holstein, was bred and raised in the Bureau's dairy herd at Beltsville, Md. Her production record made on three milkings daily at 3 years 3 months of age was 14,295 pounds of milk and 463 pounds of butterfat. She had been dry for 22 days at the time of slaughter, and was not pregnant. She was slaughtered because of a relaxed condition of the sacroiliac joint. Ante-mortem measurements in regions of the body likely to be affected by this condition were taken on the uninjured side. Though some of the carcass measurements may have been slightly affected, the resulting error is believed to be of little importance. On ante-mortem examination the quantity of mammary-gland tissue appeared to be small. The quality was very high (the highest in the entire group compared in this study) and the udder covering was extremely loose. The fiber was comparatively abundant, rather finely divided, and of medium harshness, and the free space was next to the highest in the entire group. Grades were not assigned to the size of the openings into the cisterns. Though not a large udder, its empty weight was next to the highest, its capacity was the highest, and its relation of capacity to weight was next to the highest in the entire group of udders compared.

Gross anatomy (pl. 16).—Although the udder was slightly thawed on the surface, the saw cuts were fairly smooth. Aside from a very small area at the extreme top, practically the entire surface of each section consisted of gland tissue. The rear cistern was very small

and the front one was almost lacking. There seems to be no relation between size of cistern and amount of free space in this udder. The cisterns were smaller than the teat canals. The tissue was of medium density, inclined to be wet but had a fairly good body, and contained a large proportion of clearly visible connective tissue of medium coarseness. The openings into the cisterns were of medium size.

Histology.—This was considered a nonactive or dry udder, and with the exception of a number of scattered lobules the histological examination showed the gland to be largely in the resting state. Round cell infiltration was noted in all of the sections and a limited number of the alveoli contained pus cells. A number of milk concretions were seen in some of the sections. The area illustrated in plate 17 was taken from the lower part of the left front quarter.

General.—The records show that at one time there had been inflammation in the right rear quarter, but the udder appeared to be sound when examined before slaughter. Post-mortem examination failed to show any indications that this inflammation had been present. The abundance of tissue was rated as low on ante-mortem examination but appeared to be fairly abundant in the gross sections. Judgment as to abundance of fiber and presence of fat in the udder before death is rather well supported by gross anatomical findings.

HOLSTEIN COW NO. 827

Cow 827, a registered Holstein, was bred and raised in the dairy herd at the Beltsville Experiment Station. Her production record made on three milkings daily at 2 years 7 months of age was 14,257 pounds of milk and 522 pounds of butterfat. She had been dry for 7 months 12 days at the time of slaughter, and was not pregnant. On ante-mortem examination the udder showed only a very small quantity of gland tissue, indicating a high degree of involution since the udder went dry. In quality this udder ranked second from the highest in the group compared in this study. The fiber appeared to be above medium in abundance, and medium in coarseness. The openings from teat canals to cisterns appeared to be small in front and medium in the rear. The free space was the highest in the entire group, though there were no indications of large cisterns. Though this udder was small in size, its empty weight was third, its capacity was second, and its relation of capacity to weight was third from the highest in the entire group of udders compared.

Gross anatomy (see pl. 18).—A considerable quantity of fat was present in all sections. In the sections carrying the front and rear teats and in other sections through the middle part of the udder there were fairly large areas of fat near the top, and a strip along the periphery—under the skin—which apparently consisted chiefly of a loosely formed fibrous structure, giving the appearance of the skin breaking away from the gland tissue. This suggests the possibility that a pocket of formalin may have been formed in this area at the time of filling, and that the capacity of the udder as recorded may be a trifle high. It is worthy of note, however, that the histological study showed large replacements of gland tissue with fat near the periphery. There was no distinctly circumscribed cistern in either the front or rear quarter, though numerous medium-sized ducts were present in the area usually occupied by the cistern. The cisterns

were small in total volume and very much divided. The opening from teat canal to cistern was about average in the rear quarter and slightly larger in the front quarter; and both openings were larger in diameter than the cisterns themselves. The tissue was low in porosity, about average in firmness, wet, and the visible connective tissue was abundant. The tissue appeared to be found in all parts.

Histology.—This was a small, nonlactating udder, with considerable fat. Histologically the general structure of the udder showed little deviation from the normal. The glandular portion was found to be in the resting state. Practically all the lobules showed the deposition of fat to a greater or less extent, and some of the lobules, toward the periphery of the organ, were largely replaced by fat. The udder showed a rather heavy fibrous structure throughout, with wide bands of fibrous tissue separating many of the lobules. The area illustrated in plate 19 was taken from the upper portion of the left rear quarter.

General.—There is no record of this cow having had any udder disturbance requiring treatment. Ante-mortem judgment as to abundance of fiber is well supported by both gross anatomical and histological findings. The free space did not bear a close relation to size of cisterns, but the size of cisterns was found to be much as described on ante-mortem examination. The ante-mortem observations would indicate a smaller quantity of fat than was found in both the gross and histological sections.

ABERDEEN ANGUS COW A–300

Cow A–300, a registered Aberdeen Angus had been a persistent breeder and a consistent winner in the show ring for a number of years, but nothing is known of her milk-producing ability. She had been nonlactating for about 25 months when slaughtered, and was not pregnant. Ante-mortem examination of the udder indicated a quality close to the medium, a very loose covering, a medium quantity of gland tissue, a comparatively small quantity of rather coarse fiber, and slightly more than average free space. The udder was described as fatty. Grades were not assigned to indicate the size of openings between the teat canals and the cisterns. Though only medium in size it was the highest in the entire group in empty weight; sixth from the highest in capacity, and the lowest of all in relation of capacity to weight, indicating that the udder consisted largely of material other than gland tissue.

Gross anatomy (pl. 20).—Aside from a small area above the rear teat, practically the entire udder consisted of fat. In the front quarter the gland tissue was little more than sufficient to enclose the duct or cistern, which was not more than a quarter of an inch in diameter, horizontal in position, and approached the teat canal from the rear. The rear quarter contained an area of gland tissue of irregular shape, about 5½ inches at its maximum height, about 3 inches at its maximum width, and surrounded laterally and superiorly with solid fat. The rear cistern was very small and somewhat divided. The front one was almost entirely lacking. The opening from teat canal to cistern was only moderate in size in the rear and extremely small in the front quarter. There were only a few small ducts except in the immediate vicinity of the cistern. A fairly liberal quantity of comparatively finely divided connective tissue was visible. The sections were firm when kept at low temperatures, but, owing

to the very great proportion of fat, became soft at higher temperatures. The fatty areas as well as the areas of gland tissue contained a considerable quantity of connective tissue or fiber. As the fatty areas receded these stood out in relief, giving the sections a rough appearance, particularly in the photographs.

Histology.—This udder showed an extreme fatty condition in the gross specimen and it was possible to obtain sections from only one area in the lower portion of the rear quarter. Histologically this area was found to be in the complete resting state and quite fibrous. The fibrous condition may have been due in part to the advanced age of the animal. A number of milk concretions were noted in the section. (See pl. 21.)

General.—Undoubtedly this udder had the largest proportion of fat to gland tissue of any udder yet studied. In making the antemortem observations the udder was described as fatty but the condition was underestimated. Probably because of the extreme fatty condition the quantity of fiber as shown by both gross and histological sections was also underestimated. The gross anatomical and histological findings are in very close agreement. The high condition of this cow and the 25 months dry period probably account for the large amount of fat in the udder, but the extremely small quantity of gland tissue would appear to have made it impossible for her to secrete any considerable amount of milk.

DISCUSSION AND SUMMARY

The milk- and butterfat-producing ability of four Hereford cows maintained under dairy-herd conditions is compared with that of two registered Holstein cows. A comparison is also made of the weight and measurements of the body, the weight and measurements of the internal organs and body parts, and the mammary-gland development and udder structure of the four Hereford cows, the two registered Holstein cows, three Hereford cows kept under typical beef-herd conditions, and an aged Aberdeen Angus cow.

The average production of the four Hereford cows (that were accustomed to conditions of dairy-herd management prior to their first calving and milked and fed under the same environmental conditions as the dairy herd) was 557.45 pounds of milk, testing 4.96 percent butterfat and containing a total of 27.66 pounds of butterfat. The average lactation period was 211 days. The average production of the two Holstein cows was 14,276 pounds of milk, testing 3.45 percent butterfat and containing 492.5 pounds of butterfat. The average lactation period was 364 days. The production of the two Holstein cows was 2,461 percent greater in milk and 1,681 percent greater in butterfat than the average production of the four Hereford cows.

Although the four Herefords milked in the dairy barn were considerably undersized, they could hardly have failed to make a more creditable showing, considering their opportunities both before and during lactation, if their inheritance had included the capacity for abundant lactation or the stimulus to continue lactation over an extended period. Apparently they did not possess these qualities.

In live weight and in every body dimension measured before slaughter, the Herefords studied were smaller than either the Holsteins

or the Aberdeen Angus. Though heavier, the Aberdeen Angus was smaller than the Holsteins in the measurements of length and height, but greater in some other measurements, particularly those of width and circumference of body that are affected to the greatest extent by fleshing. In this connection, attention is called again to the possible effect of age differences on the comparisons of absolute values of weight or measurements for different breeds.

When the ante-mortem data are compared on the basis of ratios based on height at withers or on length of head, a marked similarity is shown in the body proportions of the Holsteins and the Herefords. The ratio for width of fore chest appears to be the outstanding exception. For the measurements of height and length, which indicate "scale", the body proportions of the animals in all three breeds are similar. The outstanding differences in body proportions are associated with those measurements, such as width and circumference of barrel, that are most directly affected by deposition of fat. This supports the finding of a previous investigation that the cows of different breeds are generally similar in skeletal structure—the differences in type, resulting from breeding and selection, being due primarily to the degree of fleshing.

Although the contour areas for fore chest and paunch increased progressively in size from Hereford to Holstein to Aberdeen Angus and there was considerable difference in shape of the contours, only a slight difference existed in the proportion above and below the vertical midpoint.

The body surface area was almost the same for Holsteins and Aberdeen Angus. That for the Herefords was much less.

The volume of barrel also was nearly the same for Holsteins and Aberdeen Angus. That for the Herefords was very much less.

The thoracic index decreased with considerable regularity from Herefords to Holsteins to Aberdeen Angus, indicating that the Holsteins were intermediate and the Aberdeen Angus was the highest in proportion of width to depth of fore chest.

Abdominal indexes were nearly the same for all three breeds.

The legginess was almost the same for the Holsteins as for the Herefords, but much lower for the Aberdeen Angus.

Great differences existed in wedge shape. The Herefords had very little vertical wedge shape, the Holsteins had more than 10 times as much as the Herefords, and the Aberdeen Angus had more than three times as much as the Holsteins. In lateral wedge shape there was a marked decrease from Herefords to Holsteins to Aberdeen Angus. In circumference the wedge shape was almost the same for the three breeds; and on the basis of contour areas the Herefords and the Holsteins were almost the same, but the Aberdeen Angus was distinctly less. The Aberdeen Angus was very wide in the fore chest as compared with the animals in the other breeds. Again the influence of fleshing—especially in the region of the fore chest—is shown in the values for wedge shape.

With few exceptions the post-mortem data, expressed in actual units of weight or measurement, are distinctly lower for the Herefords than for the Holsteins—the most marked differences being in the visceral fats, the endocrine glands, and the udder. A comparison of the Aberdeen Angus with the Herefords shows relationships that are similar to the Holstein-Hereford relationships in most respects.

However, in comparing the Aberdeen Angus with the Holsteins, although the four greatest differences are in weights of adrenals, udder, kidneys, and thyroid, all of which are greater for the Aberdeen Angus, the data for the Aberdeen Angus are actually lower than for the Holsteins for more than two-thirds of the items.

When considered in relation to the empty body weight of the animal, there was a definite tendency for most of the weights and measurements of the internal organs and body parts to be greater for the Herefords than for either the Holsteins or the Aberdeen Angus and greater for the Holsteins than for the Aberdeen Angus, except for the visceral fats, the udder, the ovaries, the kidneys, and some of the endocrine glands.

When grouped on the basis of anatomy and function, it appears that the organs and parts of both the Holsteins and Aberdeen Angus averaged greater in actual magnitude than those of the Herefords, while those of the Aberdeen Angus averaged smaller than those of the Holsteins in the circulation and respiration group and in the digestion group. In proportion to their empty body weight, however, the Herefords had larger organs than the Holsteins in all except the endocrine gland and visceral fats groups, and larger organs than the Aberdeen Angus in all except the urogenital, endocrine gland, and visceral fats groups. The Holsteins had larger organs than the Aberdeen Angus in all except the urogenital and endocrine gland groups. The effect of fleshing is clearly indicated, for as it increases the total animal structure, the organs become proportionately smaller. The only group consistently overcoming this factor, showing greater average values for Holsteins than for Herefords and greater values for the Aberdeen Angus than for either Herefords or Holsteins, was the one consisting of endocrine glands.

Despite the breed differences in size of internal organs and body parts, there was very little difference in dressing out percentage between the Herefords and the Holsteins. The dressed weight was 50.0 percent of the live weight obtained immediately before slaughter for the four Herefords in group 1 (dairy management), 49.9 percent for the three Herefords in group 2 (beef management) and 54.7 percent for the two Holsteins. When based on empty body weight instead of live weight, the dressing out percentages were 60.2, 60.1, and 62.5, respectively. Owing to the difference in procedure incidental to the preservation of her skeleton, the carcass weight of the Aberdeen Angus cow could not be determined.

Five of the seven Herefords were extremely deficient in mammary-gland development. The other two, though more advanced, still were distinctly deficient. The greater udder development of H–16 and H–17 as compared with the other Herefords is shown both by the photographs of the living animals (figs. 1 and 2) and by the photographs of the gross sections of the udders (pl. 1). This difference may be due partly to their greater size and presumably more advanced age and partly to the fact that they came from a different line of breeding and had a different inheritance. Only two Herefords, one that nursed her calf until 18 days before slaughter, and one in advanced pregnancy, showed signs of activity in the gland tissue, and all except these two showed large quantities of fat deposits in the histological sections. The udder of the Aberdeen Angus was much larger and appeared to have a greater quantity of gland tissue, but on post-

mortem examination it proved to consist chiefly of fat. The Holsteins had udders of comparatively small size for the breed.

The Holsteins ranked considerably above the Herefords in most of the udder characteristics associated with "udder quality". The Aberdeen Angus ranked close to the Herefords in most of these items but above the Holsteins in a few. There was little difference between the breeds in those items that might be considered antagonistic to quality. Grades for milk veins and milk wells were in most cases definitely higher for the Holsteins than for the other breeds. Though the grades for quality of udder are in most cases higher for the Holsteins than for either the Herefords or the Aberdeen Angus, the differences do not approach the very great difference in producing capacity that actually existed between the Holsteins and the Herefords, and that in all probability existed between the Holsteins and the Aberdeen Angus.

In size (empty weight) of udder the Herefords in group 2 (beef management) differed from the Herefords in group 1 (dairy management) by only 2.30 percent; the Holsteins were 160.16 percent greater than the Herefords; and the Aberdeen Angus was 336.08 percent greater than the Herefords and 67.62 percent greater than the Holsteins. The comparatively high weight of udder in the Aberdeen Angus was due to excessive deposition of fat.

In capacity of udder the Herefords in group 2 (beef management) averaged 53.32 percent more than the Herefords in group 1 (dairy management). This may indicate a possibility that the Herefords in group 2 produced more abundantly than those in group 1. Actual milk production records for the cows in group 2 are not available, of course, but there is nothing in the appearance of the gross sections of the udders to indicate they had a greater quantity of mammary-gland tissue. The udder capacity of the Holsteins was 520.33 percent greater than the average for the Herefords, and 359.78 percent greater than for the Aberdeen Angus. The capacity of the Aberdeen Angus, however, was 34.92 percent greater than the average for the Herefords. The proportion of mammary-gland tissue in the udder of the Aberdeen Angus was extremely small. The low udder capacity of cows of the beef breeds studied was shown consistently.

In "relation of capacity to weight" of udder, the Herefords in group 2 (beef management) averaged 74.86 percent higher than those in group 1 (dairy management). The Holsteins exceeded the Herefords by 130.12 percent, but the Aberdeen Angus was 69.96 percent lower than the Herefords and 86.95 percent lower than the Holsteins. The low fluid-holding capacity per unit of weight for the beef-cow udders indicates a small quantity of gland tissue in proportion to fat or connective tissue. This was particularly true of the Aberdeen Angus, which had the heaviest udder with a capacity only slightly above the average for the Herefords, and the lowest relation of capacity to weight of all the udders included in this study. The effect of heavy fat deposition in the udder of this cow is clearly indicated, but the extent to which her long dry period was responsible for it is not definitely known.

For the six cows in this study having records of production there appears to be a high positive correlation between size (empty weight), capacity, and ratio of capacity to weight of udder and the quantity of milk produced, if the two Holsteins, the highest producing Hereford,

and the three lowest producing Herefords are considered as groups, but little if any correlation among the three lowest producing individual Herefords. Though the Holstein udders exceeded the Hereford udders by 163 percent in empty weight, 661 percent in capacity, and 204 percent in ratio of capacity to weight, these differences do not approach the corresponding differences of 2,461 percent and 1,681 percent, respectively, for milk and butterfat production. At the same time the percentage differences for udder size and capacity were much more significant of the producing ability than were the udder characteristics studied on the living animals. This is in harmony with previous studied, which showed size and capacity of udder were the only items of those studied that had significant correlations with records of production.

With few exceptions the antemortem observations were fairly well supported by the findings reported in the gross anatomical and histological studies, and the gross anatomical observations are perhaps even more closely supported by the histological findings.

The proportion of fat in the udder of the Aberdeen Angus was extremely high. The possible effect of prolonged inactivity on fat deposition has been discussed. In the Herefords it was high but less extreme. One of the Holstein udders had practically no visible fat in the gross sections, the other a moderate quantity. Though in a few instances the proportion of visible fat in the udders of the Herefords was comparatively small, the total quantity of gland tissue and the measured capacity of the udder were both so small that it is inconceivable they could have produced milk in abundant quantities. To this extent the findings with Herefords support the observations and conclusions previously reported for the Aberdeen Angus, which were to the effect that cows of the specialized beef breeds do not inherit a mammary development sufficient to enable them to be liberal milk producers.

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GROWTH AND DEVELOPMENT OF DICTYOSTELIUM DISCOIDEUM WITH DIFFERENT BACTERIAL ASSOCIATES [1]

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INTRODUCTION

The genus *Dictyostelium* and the group to which it belongs have been known since Brefeld (*2*) [3] described *Dictyostelium mucoroides* in 1869. Additional species have been added to the genus by Van Tieghem (*22*), Marchal (*10*), Olive (*13*), and Raper (*18*).

The developmental history of species of the Dictyosteliaceae is well known from the works of Brefeld (*2, 3*), Van Tieghem (*22, 23*), Olive (*14*), Harper (*6, 7, 8*), and Raper (*18*). Their investigations dealt either with the taxonomy of the group or with the formation of fruiting structures in certain species of the family, whereas little study was given to the vegetative stage and no attention was paid to the role of the bacteria that accompanied the slime molds. Some investigations of a physiological nature, however, were made by Nadson (*12*), Potts (*17*), Vuillemin (*24*), Pinoy (*15, 16*), and Skupienski (*20, 21*); and in their studies the role of the accompanying bacteria rightfully occupied the center of attention.

The relation between species of the Dictyosteliaceae and the bacteria with which they are associated has been a subject of dispute. Although any effective study of this relationship obviously would have to be made with the slime molds growing in association with pure cultures of bacteria of known identity, only a part of the studies previously reported were made with such cultures. Further, there is a disparity in the results reported by different investigators working with the same species of *Dictyostelium* in association with the same species of bacteria.

Because of the conflicting results reported by earlier students of the Dictyosteliaceae and because of the limited scope of their investigations, the need for additional study of the whole question of the relationship between species of this family and the bacteria that accompany them became apparent. The writer, therefore, undertook the investigation of this problem with the following objectives in view: (1) To study the range of different species of bacteria in

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[3] Reference is made by number (italic) to Literature Cited, p. 314.

association with which a representative member of the Dictyosteliaceae could grow; (2) to study the manner in which myxamoebae of such a species feed upon bacteria; and (3) to study the relation between a species of the Dictyosteliaceae and the bacteria associated with it.

Dictyostelium discoideum Raper was selected for this study because of the unique advantages for experimental studies which it affords.

LITERATURE REVIEW

Brefeld (*2*), Van Tieghem (*22*), Olive (*14*), and Harper (*6*) noted the presence of bacteria in their cultures of species of the Dictyosteliaceae but did not understand the role played by the bacteria in the nutrition of the myxamoebae, nor did they know the identity of the bacteria that accompanied their cultures. Brefeld (*2*) noted the ingestion of solid particles by the myxamoebae of *Dictyostelium mucoroides*. Van Tieghem (*22*) and Olive (*14*) observed the actual ingestion of bacteria by myxamoebae of the Dictyosteliaceae, but both investigators believed this phenomenon to be without significance and concluded that the myxamoebae fed upon nutrients in solution. Inasmuch as the emphasis in their studies was placed on the fruiting stage, which involves the final orientation and differentiation of myxamoebae into a fruiting structure, rather than on the vegetative stage, which involves the growth and multiplication of myxamoebae, this lack of appreciation of the role of bacteria is understandable.

Nadson (*12*) was the first to call attention to the association of a known species of bacteria, *Bacillus fluorescens liquefaciens*, with a species of the Dictyosteliaceae, *Dictyostelium mucoroides*. He considered that the two organisms were symbionts and that the bacteria favored the slime mold by creating an alkaline reaction in the culture medium. The myxamoebae, he believed, fed solely upon nutrients in solution.

In his extensive study of the physiology of *Dictyostelium mucoroides*, 3 years later, Potts (*17*) observed that the myxamoebae of *D. mucoroides* were dependent upon the presence of bacteria for their nutrition and growth, and further that colonies of bacteria were consumed by the slime mold. He did not observe the ingestion of bacteria by the myxamoebae, however, and concluded that the myxamoebae excreted an enzyme, which digested the bacterial cells outside the bodies of the myxamoebae, and subsequently incorporated in solution the products of their decomposition. Using maize extract agar, he was able to grow *D. mucoroides* in association with pure cultures of *Bacillus megatherium*, *B. subtilis*, and *B. fluorescens liquefaciens*, in addition to *Bacterium fimbriatum* Potts with which he originally isolated the slime mold. Potts found no indication of a symbiotic relationship between the slime mold and the associated bacteria.

Vuillemin (*24*) isolated and cultivated *Dictyostelium mucoroides* in association with *Bacillus fluorescens non-liquefaciens*, but could not grow the same slime mold in association with *B. pyocyaneus*. He (*24*) reported that the slime mold acted as a "bacteriophage" and that the myxamoebae of this species ingested bacterial cells and digested them in vacuoles within the bodies of the myxamoebae. In the same year, Pinoy (*15*) reported successfully cultivating *D. mucoroides* in association with, or, as he termed it, in "pure-mixed culture", with *Micro-*

bacillus prodigiosus and *B. coli communis* in addition to *B. fluorescens liquefaciens*, which had been associated with the slime mold in his original isolation. Four years later (*16*) he added five additional Gram-negative bacteria to the list with which *D. mucoroides* could grow, but reported that it could not grow with Gram-positive species or, as Vuillemin (*24*) had indicated before him, with *B. pyocyaneus*. Pinoy (*16*) made an intensive study of the ingestion and digestion of bacterial cells by the myxamoebae of *D. mucoroides*. He succeeded in extracting from large numbers of myxamoebae a preparation which (1) liquefied gelatine and (2) dissolved bacterial cells (*B. coli communis*) that had been killed by chloroform. To the active substance, or enzyme, contained in this extract, he gave the name "acrasidiastase", and noted that on the whole it was similar in its action to a substance, or enzyme, earlier isolated by Mouton (*11*) from a soil amoeba and termed by him "amibodiastase." Pinoy (*16*) considered the slime mold as living parasitically upon the colonies of the associated bacteria.

Skupienski (*20, 21*) likewise isolated *Dictyostelium mucoroides* in association with *Bacillus fluorescens liquefaciens* and cultivated the two organisms in pure-mixed culture. Like Vuillemin and Pinoy, he reported the ingestion and digestion of bacterial cells by the myxamoebae of *D. mucoroides*, but believed nonetheless that the two organisms were symbionts.

In 1935 the writer (*18*) described *Dictyostelium discoideum*, a new species characterized by (1) migration, (2) upright sorocarps, and (3) discoid base, pointing out that this species was accompanied by bacteria and that the myxamoebae reached their maximum development within the bacterial colonies, and, indeed, occurred outside the limits of such only as scattered myxamoebae. However, neither the relation between the myxamoebae and the bacteria nor the identity of the associated bacteria was then known. Since that time these points have been cleared up in large measure, and this work is reported and discussed herein.

HOST RANGE OF DICTYOSTELIUM DISCOIDEUM

DICTYOSTELIUM DISCOIDEUM IN ASSOCIATION WITH VIBRIO ALKALIGINES

Using the type strain of *Dictyostelium discoideum* (*18*), the writer isolated the bacteria associated with this slime mold and found that it was accompanied by a single species of bacteria, *Vibrio alkaligines* Lehm. and Neum.[4] When grown upon hay-infusion agar this bacterial culture produces raised, somewhat slimy colonies, which more or less retain their general character even when a rich growth of *Dictyostelium* occurs within them.[5]

In culturing *Dictyostelium discoideum* in association with *Vibrio alkaligines* upon hay-infusion agar, the usual method of transfer was to remove loopfuls of bacteria and *Dictyostelium* from well-established cultures and to streak these upon the surface of fresh agar plates.

[4] Identified by N. R. Smith.

[5] As will be seen from the discussions that follow, this was not the case with the majority of bacterial species that were subsequently studied in association with *D. discoideum*, for in the greater percentage of cases the bacterial colonies were completely consumed by the feeding myxamoebae. The fact that the myxamoebae of *D. discoideum* only partially consume the colonies of *Vibrio alkaligines* explains in large measure why the writer overlooked the true relation between the myxamoebae and the associated bacteria during his early studies with this slime mold.

When this method was employed, good growth of bacteria and of *Dictyostelium* was invariably obtained. However, when care was taken to transfer only the spores from single sorocarps, growth of the *Dictyostelium* was not uniformly obtained but occurred at some points of inoculation and not at others. Further, in these cultures it was observed that the two organisms always grew at the same points and that neither ever developed alone. The explanation of this phenomenon was not at first obvious, but later experiments proved that the slime mold was dependent upon bacteria for nutriment, a fact which was in agreement with results earlier obtained by Potts (*17*) and Pinoy (*16*) with *D. mucoroides*.

From the foregoing results it was obvious that bacteria-free spores had been inoculated at some places but not at others. In order to determine the character and position of the sorocarps bearing spores that were free of bacteria, inoculations were again made with spores only, and care was taken to inoculate some plates with spores taken from sorocarps that had been formed outside the limits of the bacterial colonies in which the pseudoplasmodia had developed, while other plates were inoculated with spores taken from sorocarps that had been formed within the limits of the bacterial colonies.[6] It was found that bacteria and *Dictyostelium* grew at all points of inoculation in plates that had been seeded with spores obtained from sorocarps located within the bacterial colonies, but occurred at only 1 of 10 points of inoculation in plates that had been seeded with spores obtained from sorocarps located outside the bacterial colonies. Subsequent experiments of this type demonstrated that if spores were taken only from sorocarps which had formed at a distance of 0.5 cm or more beyond any evidence of bacterial growth then the spores were in all cases free from bacteria.

Such bacteria-free spores germinated, but the emergent myxamoebae failed to grow in the absence of bacteria. However, it was only necessary to add bacteria to any point at which pure spores had been inoculated in order to secure an immediate growth of *Dictyostelium discoideum*.

The pseudoplasmodia were positively phototactic, and when cultures were placed in one-sided illumination the pseudoplasmodia migrated toward the light. Under favorable culture conditions a large percentage of the resulting sorocarps were formed at distances of 1.0 cm or more from bacterial colonies in which the pseudoplasmodia developed. In migrating this distance, the pseudoplasmodia divested themselves of all bacteria that were originally either contained inside or attached to the pseudoplasmodia at the time they left the bacterial colony. *Dictyostelium discoideum* is the only species of the Dictyosteliaceae that possesses a migrating pseudoplasmodium and is, therefore, the only species that regularly bears bacteria-free spores. The pure spores borne in isolated sorocarps that are formed from migrating pseudoplasmodia can be inoculated at will with a pure culture of any bacterium, and the growth and development of *D. discoideum* in association with that bacterium can be studied in what Pinoy, Skupienski, and other workers have called a "pure-mixed culture."

[6] In *D. discoideum* (*18*), after the myxamoebae comprising the pseudoplasmodia have crowded together into compact, cylindrical, tapering masses, these masses, or pseudoplasmodia, characteristically move outside the bacterial colony as units and continue to migrate for a greater or less distance before forming sorocarps. At the same time, other pseudoplasmodia fail to migrate and hence form sorocarps within the limits of the bacterial colony.

PRELIMINARY STUDIES WITH CERTAIN SAPROPHYTIC BACTERIAL ASSOCIATES

Since members of the Dictyosteliaceae had been isolated almost exclusively with fluorescent bacteria by earlier investigators (*12*, *15*, *20*, *24*) and had been successfully grown in association with these bacteria by Nadson (*12*), Potts (*17*), Vuillemin (*24*), Pinoy (*15*, *16*), and Skupienski (*20*, *21*), the writer early turned to a study of *Dictyostelium discoideum* in association with *Pseudomonas fluorescens* Migula.[7] Following this, the slime mold was cultivated in association with an additional species of Gram-negative bacteria, *Escherichia coli* (Migula) Castellani and Chalmers, and with two Gram-positive species, *Bacillus megatherium* De Bary and *B. subtilis* Cohn. With each of these common saprophytic species, *D. discoideum* grew somewhat better than in control cultures with *Vibrio alkaligines*. Thus *D. discoideum* grew better in association with other bacterial species than that with which the slime mold was originally associated.

In the above-mentioned cultures with common saprophytic bacteria and in those with *Vibrio alkaligines*, the mature sorocarps varied greatly in size but were always of essentially the same pattern, characterized by upright, straight, sinuous, or loosely spiral sorophores, which arose from circular and expanded or cone-shaped basal disks and bore at their apices grayish-white to pale lemon-yellow sori of slightly elliptical form. Under favorable conditions such as existed in these cultures, the differentiation of myxamoebae in the developing sorocarp into stalk cells and spores progressed at a proportional rate, so that, regardless of the size of the fructification, the ratio of sorophore (stalk) to sorus (spore mass) size remained relatively constant. This condition is well illustrated by the camera lucida drawings of mature sorocarps of normal pattern shown in figure 1, *A–D*. For a detailed account of sorocarp formation, the reader is referred to the original description of *Dictyostelium discoideum* (*18*).

The preliminary studies clearly demonstrated: (1) That *Dictyostelium discoideum* could grow, and grow well, in association with bacteria other than that with which the original culture was associated; (2) that *D. discoideum* could grow alike with Gram-negative and Gram positive bacteria; (3) that hay-infusion agar provided a satisfactory medium for cultivating *D. discoideum* in association with different bacteria; (4) that the sorocarps produced in cultures with different bacteria presented essentially the same pattern; and (5) that the ratio of sorophore to sorus size remained relatively constant regardless of the size of the sorocarp. Therefore, it was recognized that *D. discoideum* afforded a particularly favorable species with which to study quantitatively the growth of a species of the Dictyosteliaceae in association with a large number of different bacteria belonging to diverse groups.

METHODS DEVELOPED FOR MAKING GROWTH COMPARISONS

For these comparative studies of the growth of *Dictyostelium discoideum* in association with various bacteria, hay-infusion agar was used, the composition [8] being kept as constant as possible.

[7] In discussing the writer's work, the nomenclature for the bacterial species studied is in all cases according to Bergey (*1*); whereas, in reviewing the work of earlier investigators, the nomenclature used by those investigators is followed.

[8] The hay-infusion agar was prepared in the following manner: 35 g of partially decomposed hay infused in a liter of tap water for one-half hour in an autoclave at 110° C. and 5–10 pounds pressure; infusion filtered, and filtrate made up to 1 liter; 0.2 percent K_2HPO_4 and 1.5 percent agar added; adjusted to pH of 6.0–6.2; and sterilized at 15 pounds pressure for 20 minutes.

Triplicate plates of hay-infusion agar (each plate containing approximately 20 cc of medium) were inoculated with each of the cultures listed in tables 1 and 2. Inoculations were made in the following manner: Six giant colonies were established at regular intervals in a circle near the periphery of the plate, and a single colony was planted in the center; the inoculations were made with a small loop, and for each colony the inoculum was spread over an area of approximately 1 cm^2. In all cases the cultures were allowed to grow at room temperature of 22–24° C. for 2 to 3 days prior to the introduction of pure spores of *Dictyostelium*. The spores used as inoculum were obtained from sorocarps that had developed 0.5 cm or more beyond any evidence of bacterial growth. As an added precaution, spores from only one sorocarp were introduced into each bacterial colony, so that if contaminating bacteria were in any case introduced with the inoculum they would not be added to more than a single colony. Spores were

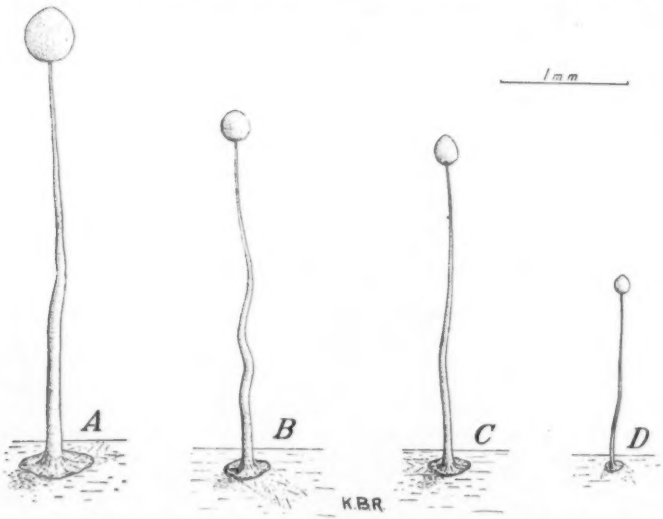

FIGURE 1.—Normal sorocarps of *Dictyostelium discoideum*: *A*, sorocarp of large size; *B* and *C*, sorocarps of medium size; *D*, sorocarp of small size. Whatever the size, the parts of the sorocarp—discoid base, tapering stalk or sorophore, and ellipsoid spore mass or sorus—are easily recognized.

introduced into each of the colonies in two of the three plates and into six of the seven colonies in the third plate. Thus for each bacterial species studied, *D. discoideum* was introduced into 20 colonies, while a single colony was reserved as a measure of the growth of the bacteria alone.

Incubation of the cultures was continued at room temperature after the spores were introduced. The cultures were observed from time to time, and a record was made of the time at which the first pseudoplasmodia began to form; and a record of the complete growth of *Dictyostelium discoideum* was made after sorocarp formation had ceased, which in the majority of cases was 6 to 8 days after the spores were added.

The total growth of *Dictyostelium discoideum* was determined by counting the number of large, medium, and small sorocarps in each of the 20 colonies of the several bacterial cultures. These counts were subsequently averaged and the growth per colony was obtained (tables 1 and 2).

For the terms "large", "medium", and "small sorocarps", used throughout this paper as a means of expressing quantitatively the growth of *Dictyostelium discoideum*, the following arbitrary limits were chosen:

(1) *Large sorocarps.*—Those with sori having a cross diameter of 250μ or more and sorophores having a length of 2.5 to 3.0 mm or more.
(2) *Medium sorocarps.*—Those with sori having a cross diameter of 150μ to 250μ and sorophores having a length of 2 to 3 mm.
(3) *Small sorocarps.*—Those with sori having a cross diameter of 75μ to 150μ and sorophores having a length of 1 to 2 mm.

Although it might seem that the number and size of the sorocarps would not serve as a reliable index of the amount of growth in *Dictyostelium discoideum*, an analysis of growth in this organism shows ample justification for such a procedure. Growth in the Dictyosteliaceae consists in an increase in the mass and in the numbers of feeding myxamoebae, that is, it is characteristic of the vegetative stage. On the other hand, the formation of the fruiting structures involves no vegetative growth but rather is a matter of development, or "integration and differentiation" as Harper (*8*) has termed it. Since this is true, it would at first seem that any comparison of growth should be limited to the vegetative stage where growth occurs. However, since no increase in the number of myxamoebae occurs after the fruiting stage is initiated and since each myxamoeba entering into a psuedoplasmodium forms either a spore or a stalk cell in the developing fructification (*2*, *3*, *6*, *14*), the identity of each vegetative myxamoeba is in fact preserved in the mature sorocarp. The vacuolate stalk cells are much larger than the spores, but since the size of the sorus and that of the sorophore remain proportional (p. 293), the relative numbers of the two cell types remain approximately constant in normal sorocarps. A sorocarp of a particular size, therefore, represents a fairly definite amount of actual growth. Since this is true, the amount of growth occurring in any bacterial colony can be expressed in the numbers of sorocarps produced in that colony, when the size of the sorocarps is considered.

The total growth of *Dictyostelium discoideum* in association with a given culture of bacteria can be satisfactorily expressed in terms of the total number of large, medium, and small sorocarps; but the growth of the slime mold with two or more different bacteria cannot be quantitatively compared in terms of the total number of sorocarps, because the numbers of sorocarps falling within the different size groups do not remain in the same ratio to one another.[9] However, such a quantitative comparison can be made and the results graphically shown, if the sorocarps of the three sizes are all converted into a common expression. As already noted, the amount of actual growth represented by a sorocarp is in direct proportion to the size of the

[9] This point is excellently illustrated by the growth and development of *Dictyostelium discoideum* with *Bacillus cereus* Frankland and Frankland and with *Sarcina lutea* Schroeter as shown in table 1. There was an average of 23 sorocarps per colony of *B. cereus* and an average of 22 sorocarps per colony of *S. lutea*; still the growth of the slime mold was almost three times as great with the latter associate (fig. 2). This apparent contradiction is explained entirely by the size distribution of the sorocarps in the colonies of the two bacteria (table 1).

sorocarp; and further, the relative proportions of sorus and sorophore remain fairly constant in a normal sorocarp regardless of the size of that sorocarp. Therefore the amount of growth represented by a sorocarp of one size can be expressed in terms of a sorocarp, or sorocarp equivalent, of another size simply by computing the volumes of their sori.

A basis for converting sorocarps of different sizes into a common expression was obtained in the following manner: (1) The average dimensions of 50 large, 50 medium, and 50 small sori were determined; (2) then, treating the sori as spheres,[10] the average volume of a large, medium, and small sorus was computed. Medium sori were chosen as the most convenient size to which to convert sorus volumes, and a medium sorus was found to be equivalent to 6 small sori and to 0.29 of a large sorus. The total amount of growth of *Dictyostelium discoideum* with the different bacteria is, therefore, expressed as medium-sorocarp equivalents wherever quantitative comparisons are made, as in figures 2 and 3.

Because of the amount of work involved, these investigations extended over a period of 6 months. However, the results obtained with the several species of bacteria could be quantitatively compared and the differences in the growth of *Dictyostelium* could be attributed either to the amount of bacterial growth present or to the ability of the myxamoebae to feed upon the bacteria, since the following factors remained constant throughout the study: (1) The culture media were approximately uniform in composition; (2) the number of bacterial colonies per plate and the area inoculated per colony were the same in all cases; (3) the cultures were all incubated at the same temperature, 22°–24° C; and (4) the bacterial colonies were all seeded with pure spores of *D. discoideum* when 2 to 3 days old.

DICTYOSTELIUM DISCOIDEUM IN ASSOCIATION WITH COMMON SAPROPHYTIC BACTERIA

A comprehensive study of the growth and development of *Dictyostelium discoideum* in association with a large number of different species of saprophytic bacteria was undertaken, and for this investigation species belonging to the following genera and families were selected: *Vibrio*, of the Spirillaceae; *Pseudomonas*, *Serratia*, *Escherichia*, *Aerobacter*, *Achromobacter*, *Cellulomonas*, and *Chromobacterium*, of the Gram-negative Bacteriaceae; *Bacillus*, of the Gram-positive, spore-forming Bacillaceae; *Rhizobium* and *Azotobacter*, of the nitrogen-fixing Nitrobacteriaceae; and *Sarcina* and *Micrococcus*, of the Coccaceae. A complete list of the species studied is given in table 1.

Inoculations with bacteria and subsequently with pure spores of *Dictyostelium discoideum* were made in the manner described above.

The cultures were observed from time to time and a record was made of the time at which pseudoplasmodium formation began, of the character of the sorocarps produced, and of the total growth of *Dictyostelium discoideum* in association with the several bacterial cultures after sorocarp formation ceased.

[10] As shown in fig. 1, *A–D*, the sori are not true spheres but are slightly teardrop or ellipsoid in shape; however, the percentage of error in computing them as spheres is small and is proportional for the different size groups.

TABLE 1.—*Comparative growth of Dictyostelium discoideum in association with different saprophytic bacteria on hay-infusion agar*

Bacterial associate			Growth of *Dictyostelium discoideum*							
					Average number of sorocarps per colony				Character of sorocarps		
Culture no.	Species according to Bergey (*1*)	Reaction to Gram stain	Extent of colony clearance	Period to beginning of pseudoplasmodium formation	Large	Medium	Small	Average number of medium sorocarp equivalents per colony	Sorophore	Basal disk	Sorus
				Days							
NC-4.1	*Vibrio alkaligines*[1]	−	Partial	3	7	27	12	53	Straight	Circular, flattened	White to pale yellow.
112	*Pseudomonas fluorescens*	−	Complete	1½–2	10	25	10	62	Straight or sinuous	Circular, expanded	Do.
75	*Pseudomonas schuylkilliensis*	−	do	2	9	22	7	55	do	Cone-shaped	Do.
76	do	−	do	2	10	16	8	52	do	Circular, flattened	Do.
110	*Pseudomonas aeruginosa*	−	Partial	3–3½	1	8	4	12	Straight	do	Do.
175	*Serratia marcescens*	−	Complete	1½–2	6	21	9	44	Straight, red in color	Cone-shaped, red	Pink to light red.
107	*Escherichia coli*	−	do	2	11	26	7	66	Straight or sinuous	Circular, expanded	White to pale yellow.
Pa	*Aerobacter aerogenes*	−	do	2½	11	18	9	58	Straight	do	Do.
P	*Chromobacterium violaceum*	−	Partial	4–5	4	13	3	28	Straight or weak spiral.	Circular, flattened	Do.
36	*Achromobacter radiobacter*	−	Complete	2	9	17	7	50	Straight or spiral	do	Do.
188	do	−	do	2	12	26	8	69	do	do	Do.
168	*Achromobacter globiforme*	−	do	2	9	22	14	56	Straight or sinuous	do	Do.
124	*Cellulomonas cellasea*	−	do	2–2½	6	17	20	41	Sinuous or spiral	do	Do.
135	*Cellulomonas liquata*	−	Partial	5		3	8	4	Straight and short	Cone-shaped	Do.
133	*Cellulomonas fima*	−	do	5		5	7	6	Straight	Circular, flattened	Do.
104	*Bacillus subtilis*	+	Complete	2–2½	10	25	11	62	do	do	Do.
161	*Bacillus megatherium*	+	do	2–2½	10	24	7	60	do	do	Do.
162	*Bacillus mesentericus*	+	do		5	11	8	30	do	Circular, compact	Do.
50	*Bacillus danicus*	+	do	2–2½	6	13	23	38	do	do	Do.
160	*Bacillus cereus*	+	Partial	3	1	9	13	15	do	do	Do.
165	*Bacillus mycoides*	+	Slight	3	1	6	8	11	do	do	Do.
450	*Rhizobium meliloti* (alfalfa)		Complete	2–2½	10	15	7	51	Straight or sinuous	Circular, flattened	Do.
240	*Rhizobium japonicum* (soybean)		Partial	2–2½	5	10	6	28	Straight or spiral	Circular, compact	Do.
11	*Azotobacter chroococcum*		do	2–2½	6	11	4	33	Sinuous or spiral	do	Yellow.
16	*Azotobacter vinelandii*		do	3	2	9	10	18	Straight	Cone-shaped	Pale yellow.
K	*Sarcina lutea*	+	Complete	2–2½	9	9	4	41	Straight or sinuous	Circular, expanded	Yellow.
43	*Sarcina flava*	+	do	5	12	26	7	69	Sinuous or straight	Circular, flattened	Pale yellow.
101	*Micrococcus* sp. (yellow)	+	do	3	8	15	4	44	Spiral	Circular, expanded	Do.

[1] Not listed in Bergey's Manual (*1*) either as a valid species or as a synonym.

The results of these studies are summarized and presented in table 1, the total growth of *Dictyostelium* being recorded in the average number of large, medium, and small sorocarps per colony and also in the average number of medium-sorocarp equivalents. A comparison of the amount of growth of *Dictyostelium* in association with the different bacteria is graphically presented in figure 2, where the average total growth per colony is expressed in medium-sorocarp equivalents.

These studies can best be considered by discussing the growth and development of *Dictyostelium discoideum* in association with particular species or groups of species of bacteria.

Dictyostelium discoideum grew well and developed normally in association with the following species of Gram-negative non-spore-forming bacteria: *Pseudomonas fluorescens*, two strains of *Ps. schuylkilliensis* Chester, *Escherichia coli*, *Aerobacter aerogenes* (Kruse) Beijerinck, *Achromobacter globiforme* (Conn) Bergey et al., and *Achromobacter radiobacter* (Beijerinck and Van Delden) Bergey et al. In all of these cases the bacterial colonies were completely consumed by the feeding myxamoebae, pseudoplasmodia began to develop within 1½ to 2½ days after the introduction of *Dictyostelium* spores, and the slime mold had virtually ceased growing by the sixth or seventh day after its inoculation. The sorocarps were entirely normal in pattern, with straight, sinuous, or loosely spiral sorophores; white to pale lemon-yellow sori; and circular and flattened or cone-shaped basal disks (fig. 1, *A–D*). In association with each of these bacterial species, the growth of *D. discoideum* was in most cases as abundant as with *Vibrio alkaligines*, the species associated with the original culture of the slime mold, and in some cases even more abundant (table 1; fig. 2).

The character of the growth of *Dictyostelium discoideum* in association with *Serratia marcescens* Bizio (*Bacillus prodigiosus* Flügge) was especially interesting. Upon hay-infusion agar this bacterial species produces a dilute-crimson pigmentation. The pigment is contained within the bacterial cells and is not water-soluble. The myxamoebae of *D. discoideum* ingest and digest the cell bodies of *S. marcescens*, but apparently cannot digest the pigment, which, as a result, collects in scattered vacuoles of varying size within the bodies of the feeding myxamoebae. These vacuoles of pigment are not excreted when the myxamoebae enter the fruiting stage, and consequently the pseudoplasmodia are distinctly red in color. This coloration persists throughout the subsequent migration of the pseudoplasmodia and even through the formation of the fruiting structures, so that the mature sorocarps are characteristically colored, varying in hue from pink to dilute red. In such sorocarps as these the spores themselves are uncolored, but the slime surrounding them contains red granules which lend a red coloration to the sorus as a whole. The coloration of the sorophore and basal disk consists of minute reddish particles which are applied to the inner surface of the walls of the cells comprising these structures. Pinoy (*16*) obtained a somewhat similar coloration in *D. mucoroides* by cultivating it with *B. kieli* (*S. marcescens*?).

After it was found that *Dictyostelium discoideum* produced red pseudoplasmodia and sorocarps when grown in association with

Serratia marcescens, a culture of *Chromobacterium violaceum* (Schroeter) Bergonzini (*Bacillus violaceus* Schroeter) was procured in the hope that fruiting structures of blue or violet coloration could be obtained in cultures with this bacterium. This objective, however, was not realized, for, although a fair growth of *C. violaceum* occurred on hay-infusion agar, no pigment was produced and the sorocarps that subsequently developed were colorless.

Colonies of *Pseudomonas aeruginosa* (Schroeter) Migula were partially consumed by the feeding myxamoebae, and the resulting sorocarps were of normal pattern. Both Vuillemin (*24*) and Pinoy (*16*) attempted unsuccessfully to cultivate *Dictyostelium mucoroides* in pure-mixed culture with this bacterial species. The difference between the results obtained by these investigators and those obtained by the writer can probably be attributed to the different media employed.

Fair growth and normal development of *Dictyostelium discoideum* occurred in colonies of *Cellulomonas cellasea* (Kellerman et al.) Bergey et al., and the bacterial colonies were wholly consumed by the feeding myxamoebae. Poor growth of *D. discoideum* occurred in association with *C. liquata* (McBeth and Scales) Bergey et al. and *C. fima* (McBeth and Scales) Bergey et al., but these cultures were particularly interesting from another standpoint. After the sorocarps matured, the *Cellulomonas* attacked the cellulose walls of the cells of the sorophores

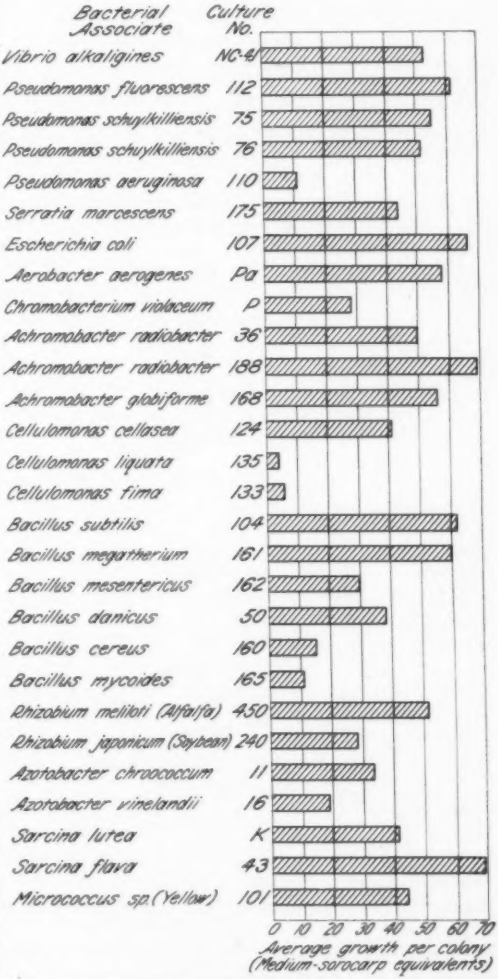

FIGURE 2.—Comparative growth of *Dictyostelium discoideum* in association with a number of common saprophytic bacteria growing upon hay-infusion agar.

and basal disks of the slime mold fructifications. In some cases all traces of cellular structure were obliterated, and the identity of the sorophore remained only as a very thin-walled hyaline tube, which contained rounded vacuoles of varying size. It may be noted that the cultures of *D. discoideum* in association with *C. fima* represent the nearest approach to a symbiotic relationship between slime mold and bacteria yet encountered among the Dictyosteliaceae, inasmuch as at first the myxamoebae fed upon the bacteria while later the bacteria decomposed the cellulose walls of the *Dictyostelium*. In these cultures, however, the growth of *D. discoideum* was so slight as to make a claim of true symbiosis untenable (table 1, fig. 2).

Among species of the Gram-positive, spore-forming bacilli, good growth of *Dictyostelium discoideum* occurred in association with *Bacillus megatherium* and *B. subtilis*, as in the preliminary studies discussed above; fair growth took place in association with *B. mesentericus* Trevisan and *B. danicus* Löhnis and Westermann; while only poor growth occurred in association with *B. cereus* and *B. mycoides* Flügge (table 1; fig. 2). The reduced growth of *Dictyostelium* in cultures with *B. mesentericus*, *B. danicus*, and *B. cereus* could largely be attributed to a smaller amount of bacterial growth and, therefore, of available food for the slime mold than was the case in cultures of *B. subtilis* and *B. megatherium*. On the other hand, *B. mycoides* grew well upon hay-infusion agar but the colonies were not noticeably cleared by the myxamoebae. The writer believes that the limited growth of the slime mold in this case can be attributed to the physical nature of the bacterial colonies. As is characteristic of *B. mycoides*, the bacilli were arranged in long chains that were not easily broken apart, and consequently the myxamoebae could not readily ingest the bacterial cells. There was no indication that the spores of any of the bacilli were digested, although in all cases they were ingested in large numbers by the myxamoebae. The sorocarps were of normal pattern in cultures with all bacilli studied.

Good growth of *Dictyostelium discoideum* occurred in association with *Rhizobium meliloti* Dangeard [11] (isolated from the nodules on the roots of alfalfa), and the bacterial colonies were completely consumed by the slime mold. On the other hand, only fair growth occurred in association with the related species *Rhizobium japonicum* (Kirchner) Buchanan (isolated from soybean), and the bacterial colonies were only partially cleared (table 1; fig. 2). No growth of *Dictyostelium* whatever occurred in colonies of *Rhizobium leguminosarum* Frank (isolated from vetch). An explanation of the lack of growth in this latter case has not yet been found; the bacteria grew well upon hay-infusion agar, and the physical character of the colonies was not essentially different from that of *R. japonicum*, in which a fair growth occurred. It is hoped that a further study of the growth of *D. discoideum* in association with different species and strains of bacteria belonging to this genus can be undertaken in the future.

Fair growth of *Dictyostelium discoideum* occurred in association with *Azotobacter chroococcum* Beijerinck, the bacterial colonies were partially cleared, and the sorocarps were of normal pattern; whereas poor

[11] The writer recognizes that members of the genus *Rhizobium* (*Bacillus radicicola* Beijerinck) are not saprophytic bacteria, but includes them here as a matter of convenience.

growth occurred in *Azotobacter vinelandii* Lipman, the bacterial colonies being only slightly cleared.

Dictyostelium discoideum grew well in association with *Sarcina lutea*, the bacterial colonies were wholly consumed, and normal sorocarps with yellow sori were produced. *D. discoideum* grew excellently (fig. 2) in association with *Sarcina flava* De Bary but developed more slowly than with *S. lutea* (table 1).

Moderately good growth of *Dictyostelium discoideum* occurred in association with a culture of a yellow *Micrococcus* (sp.?), and the bacterial colonies were completely consumed. The development of the slime mold in these cultures was especially interesting, for a large percentage of the mature sorocarps possessed closely spiral sorophores of regular and exquisite pattern.

DICTYOSTELIUM DISCOIDEUM IN ASSOCIATION WITH BACTERIA ISOLATED FROM CULTURES OF THE DICTYOSTELIACEAE

While studies with common saprophytic bacteria were being conducted, as described above, it was considered worth while to isolate the bacteria from other cultures of the Dictyosteliaceae which the writer had in culture and to attempt to grow *Dictyostelium discoideum* in association with them.

The bacteria associated with the several cultures of Dictyosteliaceae were isolated in pure culture by the dilution-plate method. The identity [12] of the bacterial cultures thus isolated, together with the name and catalog number of the culture of Dictyosteliaceae from which each was isolated, is given in table 2. From this table it will be seen that, of the writer's stock cultures of the Dictyosteliaceae, *Dictyostelium sphaerocephalum* was accompanied by three bacterial species and *Polysphondylium pallidum* (?) was accompanied by two species of bacteria, whereas all the others were accompanied by single bacterial associates. Conversely, three slime mold cultures were associated with *Vibrio alkaligines*, three with *Flavobacterium denitrificans* (Lehmann and Neumann) Bergey et al., two with *Pseudomonas schuylkilliensis*, two with *Aerobacter* or *Achromobacter* sp., and one each with *Ps. convexa* Chester, *Bacillus circulans* Jordan, and *F. buccalis* (Vignal) Bergey et al. There was no evidence pointing to an intimate relationship between the slime molds and the bacteria associated with them. It is interesting to note that *Ps. fluorescens*, which Nadson (*12*), Pinoy (*15, 16*), and Skupienski (*20, 21*) found habitually associated with *D. mucoroides* in Europe, did not occur in a single one of the writer's 10 cultures of Dictyosteliaceae from the United States (table 2).

Inoculation with bacteria and the introduction of pure spores of *Dictyostelium discoideum* into the resulting bacterial colonies were accomplished in the manner already described.

[12] Specific determinations made by N. R. Smith.

TABLE 2.—*Comparative growth of Dictyostelium discoideum in association with bacteria isolated from cultures of the Dictyosteliaceae*

Bacterial associate					Growth of *Dictyostelium discoideum*						
Species [1]	Reaction to Gram stain	Source		Colony character	Period to beginning of pseudoplasmodium formation (days)	Average number of sorocarps per colony			Average number of medium sorocarp-equivalents per colony	Character of sorocarps		
		Species of Dictyostelinaceae from which isolated	Culture no.			Large	Medium	Small		Sorophore	Basal disk	Sorus
Vibrio alkaligines	–	*Dictyostelium discoideum* Raper.	NC-4	Raised, smooth, moist	3	7	27	12	53	Straight	Circular, flattened.	White to pale lemon yellow.
Do	–	*Dictyostelium* sp.	D-8	Thin, smooth, moist	3–3½	4	30	11	46	do	do	Do.
Do	–	*Polysphondylium album* Olive or *P. pallidum* Olive.	P-8b	Raised, smooth, moist	3–3½	7	12	7	38	do	do	Do.
Pseudomonas schuylkilliensis.	–	do	P-8b	Slightly raised, smooth, glistening.	1½–2	15	29	13	83	Straight or spiral	Cone-shaped	Do.
Do	–	*D. sphaerocephalum* (Oud.) Sacc.	D-9	Thin, slightly granular, moist.	1½–2	9	20	12	53	do	Circular, flattened.	Do.
Pseudomonas convexa	–	*D. purpureum* Olive.	D-6	Raised, smooth, moist	1½–2	6	16	7	38	do	Cone-shaped	Do.
Bacillus circulans	+	*D. mucoroides* Bref.	D-91	Thin, irregular, dryish	2	6	25	24	50	Straight	Circular, flattened.	Do.
Flavobacterium buccalis.	–	*D. sphaerocephalum*	D-9	Thin, dryish, spreading	2	5	10	1	28	Straight, sinuous, or spiral.	do	Do.
Flavobacterium denitrificans.[2]	–	*Dictyostelium* sp.	D-H	do	2–2½	12	24	12	68	do	do	Do.
Do	–	*D. sphaerocephalum*	D-9	Thin, smooth, spreading.	2–2½	8	12	13	42	do	do	Do.
Do	–	*P. violaceum* Bref.	P-1	Thin, dryish, spreading.	2–2½	8	22	20	53	do	Cone-shaped	Do.
Aerobacter or *Achromobacter* sp.	–	*D. mucoroides*	D-3a	Raised, smooth, moist	1½–2	8	22	6	51	do	Circular, flattened.	Do.
Do	–	do	D-12	do	1½–2	9	26	13	60	do	do	Do.

[1] Determinations made by N. R. Smith.
[2] A form belonging to the genus *Flavobacterium* and apparently like *F. denitrificans* except that nitrates are not reduced.

The results of these studies are summarized in table 2. The time at which pseudoplasmodium formation began is recorded; the character of the sorocarps is given; and the amount of growth of *Dictyostelium discoideum* in association with the several bacteria is recorded in the average number of medium-sorocarp equivalents as well as in the average number of large, medium, and small sorocarps per bacterial colony into which *Dictyostelium* was introduced. As in the preceding studies, the values given are averages obtained from detailed counts of 20 colonies for each bacterial culture. A graphic comparison of the growth of *D. discoideum* in association with the several bacterial cultures is given in figure 3.

As shown in table 2, *Dictyostelium discoideum* grew in association with each of the bacterial cultures isolated from members of the Dictyosteliaceae. The growth of the slime mold varied appreciably with the different cultures. Considering the study as a whole, approximately average growth of *D. discoideum* occurred in association with the strain of *Vibrio alkaligines*, No. NC–4.1, which was isolated from the type culture of this slime mold.

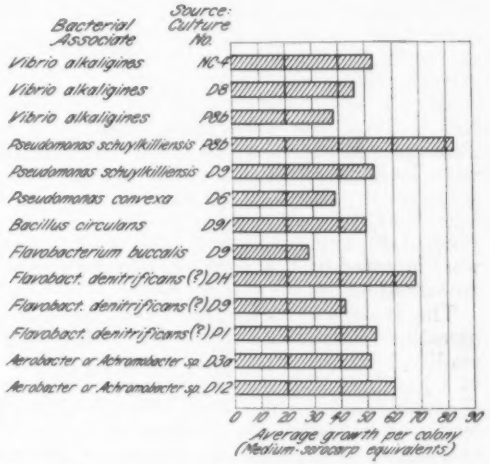

FIGURE 3.—Comparative growth of *Dictyostelium discoideum* in association with bacteria isolated from cultures of species of the Dictyosteliaceae. Cultures on hay-infusion agar.

The colonies of the three strains of *Vibrio alkaligines* studied were not wholly consumed by the *Dictyostelium*, whereas the colonies of all other bacteria isolated from members of the Dictyosteliaceae were completely devoured by the feeding myxamoebae, and the growth of the *Dictyostelium* was in direct proportion to the growth of the associated bacteria.

Pseudoplasmodia began to develop in 1½ days after spores of *Dictyostelium* were introduced into colonies of *Aerobacter* or *Achromobacter* sp. and species of *Pseudomonas*, whereas they did not appear in colonies of the three strains of *Vibrio alkaligines* until 3 days after spore inoculation. In colonies of *Bacillus circulans*, *Flavobacterium buccalis*, and *F. denitrificans*, the rate of development of the slime mold was intermediate between the above-mentioned extremes.

Normal sorocarps were produced in association with each culture of bacteria isolated from the Dictyosteliaceae. In all cases the sorocarps were characterized by evenly tapered, straight, sinuous, or loosely spiral sorophores; circular and flattened or cone-shaped basal disks; and white to pale lemon-yellow sori (table 2; fig. 1, A–D).

The growth and development of *Dictyostelium discoideum* in these cultures corresponded closely with that in cultures with common saprophytic bacteria, both with respect to the amount of growth present and with regard to the pattern of the sorocarps. There was no indication that bacteria which had been isolated from the Dictyosteliaceae were favorable for *D. discoideum* to a greater degree than common saprophytic bacteria, which, so far as known, had never been associated with a slime mold.

NUTRITION OF DICTYOSTELIUM DISCOIDEUM

FEEDING HABITS OF THE MYXAMOEBAE

Because of its large size, *Bacillus megatherium* was selected as a favorable form with which to study the manner in which myxamoebae of this group feed upon the bacteria that accompany them. Such an investigation seemed particularly pertinent because of the disparity in results obtained by Potts (*17*) and Pinoy (*16*) with the related species, *Dictyostelium mucoroides*.

Hanging-drop cultures were employed for this investigation, and hay infusion and hay-infusion agar were used as nutrient media. *Bacillus megatherium* and pure spores of *Dictyostelium discoideum* were inoculated together, and the growth of the slime mold was subsequently followed in microcultures by means of a Zeiss water-immersion lens. Corroborating the earlier work of Vuillemin (*24*), Pinoy (*16*), and Skupienski (*21*), it was found that the bacterial cells were ingested by the myxamoebae and digested in vacuoles within the amoeboid bodies.

The ingestion of bacterial cells and the subsequent progressive digestion of the same within the bodies of living myxamoebae could readily be followed. Different stages in the ingestion and digestion of cells of *Bacillus megatherium* are shown in figure 4. Figure 4, *A*, shows a myxamoeba shortly after its germination and before active feeding has begun; the hyaline ectoplasm (*ect*), the finely granular endoplasm (*end*), and the contractile vacuole (*cv*), are shown. The ingestion and digestion of bacilli by the myxamoebae of *Dictyostelium discoideum* is clearly shown in figure 4, *B*1–*B*7. The figures of this series show the same myxamoeba at approximately 10-minute intervals over a period of 65 minutes. In figure 4, *B*1, is shown a food vacuole (*v*1) of recent formation, and in the successive figures of the series the progressive digestion of the bacteria contained within it can be followed. Also shown in figure 4, *B*1, is the beginning of the ingestion of a chain of five bacilli. In figure 4, *B*2, the process of ingestion is further advanced, and in figure 4, *B*3, the first three cells of the chain have been cut off into a food vacuole (*v*2), and the digestion of the bacilli contained in it can be followed in the successive figures of the series. In figure 4, *B*4, the last two cells of the chain have been been completely ingested and are contained in a third food vacuole (*v*3) and the progressive digestion of its contents can likewise be followed.

From this series of figures a conception can be gained of the rapidity with which feeding, that is, the ingestion and digestion of bacteria, occurs; for in the course of approximately an hour, five bacilli were ingested and almost completely digested. The writer's studies indi-

cate that ingestion usually occurs at some point upon the anterior portion of the myxamoeba, but can occur and often does occur at any point upon the body surface. It should be remembered, however, that anterior and posterior regions in these amoeboid bodies mean little, since the identity of the two changes constantly.

During the digestion of *Bacillus megatherium* cells, certain changes in the form and content of the food vacuoles are regularly to be observed. These changes are shown diagrammatically in figure 4, *D*1 to *D*6. First, two bacilli are seen enclosed end to end in an elongate, ellipsoid vacuole. The vacuole tends to become spherical, and the two bacteria become separated and so displaced that they lie with their long axes either perpendicular or parallel to one another. During this time the vacuole becomes progressively smaller, and meanwhile an interesting change regularly takes place within the bodies of the

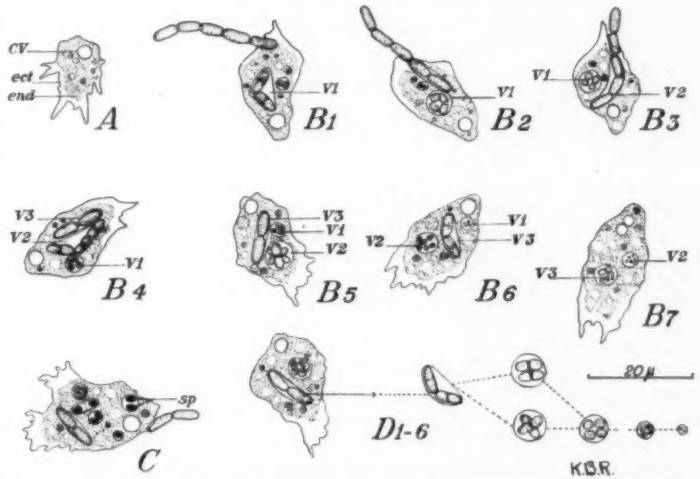

FIGURE 4.—Camera lucida drawings of myxamoebae of *Dictyostelium discoideum* feeding on cells of *Bacillus megatherium*. *A*, Young myxamoebae; *cv*, contractile vacuole; *end*, granular endoplasm; *ect*, hyaline ectoplasm. *B*1–*B*7, a feeding myxamoeba drawn at intervals of approximately 10 minutes over a period of 65 minutes; *v*1, *v*2, and *v*3, food vacuoles. *C*, Myxamoeba containing undigestible spores; *sp*, spores. *D*1–*D*6, food vacuole showing bacilli in progressive stages of digestion.

enclosed bacteria. Digestion first becomes evident near the middle region of an engulfed bacillus and becomes successively more distinct until the bacterial cell is completely digested at this point. The fractions of the original bacillus become more and more reduced in size and usually become further fragmented, while the vacuole becomes progressively smaller and finally disappears within the granular endoplasm of the myxamoeba.

Myxamoebae of *Dictyostelium discoideum* ingested and rapidly digested the vegetative cells of *Bacillus megatherium*, while the spores, although ingested in large numbers, were not digested (fig. 4, *C*).

The results of the writer's investigation upon the manner of feeding in *Dictyostelium discoideum* are in agreement with the studies reported by Vuillemin (*24*), Pinoy (*16*), and Skupienski (*21*) for *D. mucoroides*, while they were in marked disagreement with the results reported by

Potts (*17*), who reported that the bacteria were digested extracellularly by the myxamoebae of *D. mucoroides*.

In this connection it is interesting to note that in the Myxogastrales, a related order of the Mycetozoa, a somewhat similar ingestion and digestion of bacteria by the swarm cells occurs. This was first observed by Lister (*9*) and has since been studied in detail by Gilbert (*4*, *5*) and Smart.[13]

GROSS CLEARANCE OF BACTERIAL COLONIES BY THE MYXAMOEBAE

Working with *Dictyostelium mucoroides*, Potts (*17*) was the first to report the clearance and consumption of bacterial colonies by the myxamoebae of the Dictyosteliaceae, and this observation led to his discovery that *D. mucoroides* was dependent upon bacteria for its nutriment. In the case of *D. discoideum* the writer has found, as has been noted, that when spores of this slime mold are inoculated into colonies of bacteria upon hay-infusion agar the colonies are completely consumed in the majority of cases. Typically, the clearance of the colonies occurred in the following manner. After spores of *D. discoideum* are inoculated into the center of the bacterial colony, the first macroscopic evidence of the growth of the slime mold appears, approximately 18 to 24 hours later, as a small, cleared area at the point of inoculation. During the succeeding 18 to 24 hours, this area expands and the formerly smooth central area of the colony, now largely devoid of bacteria, becomes dull and minutely roughened. At the end of this period of approximately 1½ to 2 days the myxamoebae at the center of the colony begin the formation of pseudoplasmodia, and at the same time the cleared area is enlarged as the result of continued feeding by the remaining myxamoebae.

Among the factors that influence the rate and extent of clearance of the bacterial colony by the myxamoebae of *Dictyostelium discoideum*, may be listed (1) the character of the bacterial growth and (2) the composition of the underlying medium. It has already been noted that *D. discoideum* is able to feed only meagerly upon *Bacillus mycoides* because of the mycoid character of the bacterial growth and that the colonies of that species are not noticeably consumed. Also, *D. discoideum* grows poorly or not at all in bacterial colonies characterized by the presence of a large amount of gum. An investigation is now in progress on the influence of the composition of the medium on the rate and extent of colony clearance.

UTILIZATION OF KILLED BACTERIA BY THE MYXAMOEBAE

In the foregoing studies, *Dictyostelium discoideum* was in all cases grown in colonies of living bacteria, and the question arose as to whether living bacteria were essential to the growth of the myxamoebae and the subsequent development of a species of the Dictyosteliaceae. Some studies of a somewhat similar nature were made by earlier investigators. Potts (*17*) reported that *D. mucoroides* could grow upon cells of *Bacterium fimbriatum* that had been killed with chloroform but could not grow upon similar cells killed with alcohol or ether, and could not grow upon cells of *Bacillus megatherium* that had been killed by any agent. Pinoy (*16*) reported that *D. mucoroides*

[13] SMART, R. F. THE INFLUENCE OF EXTERNAL FACTORS ON THE BEHAVIOR AND DEVELOPMENT OF THE MYXOMYCETES. Unpublished Thesis, Ph. D., Harvard University. 1935.

could not grow upon cells of *Bacillus fluorescens liquefaciens* that had been killed by ether, chloroform, or other agents, and that the slime mold could grow only in the presence of living bacteria. The writer, therefore, undertook to determine whether *D. discoideum* could feed upon killed bacteria and, if so, whether normal development of the slime mold would subsequently take place.

Serratia marcescens and *Achromobacter radiobacter* were chosen for this study. Two experiments were performed, the bacteria in one being killed by heat and in the other by ultraviolet light. In the first of these experiments, colonies of the above-mentioned bacteria were allowed to develop for 3 days upon hay-infusion agar in Petri plates. At the end of that period the cultures, with the dish covers removed, were exposed to flowing steam in the autoclave for 10 minutes. The plates were then carefully removed in order that the floating bacterial colonies would not sink into the melted agar, and the medium was allowed to resolidify. To make certain the bacteria had been killed, nutrient agar tubes were inoculated with bacteria taken from the several colonies. When it was found that no viable bacteria remained, pure spores of *Dictyostelium discoideum* were introduced into the bacterial colonies. Good growth and normal development of *D. discoideum* occurred in the colonies of killed bacteria. The colonies were consumed in a manner similar to that already described for colonies of living bacteria.

In the second experiment, colonies of the above-mentioned bacteria were grown upon hay-infusion agar for 3 days and were then exposed to ultraviolet light.[14] As described above, nutrient agar tubes were inoculated with bacteria from the exposed colonies to make certain that the bacteria had been killed. Pure spores of *Dictyostelium discoideum* were then introduced into the exposed colonies and into similar colonies that had been shielded from the ultraviolet light. Better growth of *D. discoideum* occurred in the shielded (living) colonies than in the exposed (killed) colonies, but the development of the slime mold in the exposed colonies was entirely normal in character and sorocarps of normal pattern were produced (fig. 1, *A–D*).

UTILIZATION OF NUTRIENTS IN SOLUTION BY THE MYXAMOEBAE

Since the myxamoebae of *Dictyostelium discoideum*, contrary to what Pinoy (*16*) reported for *D. mucoroides*, were not obligately dependent upon living bacteria, the problem arose as to whether bacteria were really essential for the growth and development of species of *Dictyostelium*. Although limited time has prevented the writer from investigating this point exhaustively, some pertinent information has been obtained.

Bacteria-free spores of *Dictyostelium discoideum* were repeatedly inoculated upon various infusion media made from hay, dung, potatoes, carrots, peas, mushrooms, or yeast, and upon a number of synthetic media containing varying amounts of peptone and some carbohydrate. With two exceptions, no growth whatever of the *Dictyostelium* occurred in such cultures in the absence of bacteria, and in the two exceptions the growth of the slime mold was very slight. These exceptions occurred under the following circumstances: (1) Upon an agar medium made from the broth of canned green peas, a very limited vegetative

[14] The writer is indebted to Dr. William Arnold for making the light exposures.

growth of the myxamoebae occurred; the myxamoebae, however, remained widely scattered and no pseudoplasmodia whatever were produced. (2) A very limited growth of *D. discoideum* occurred in the absence of bacteria upon media containing 1 percent of lactose and from 3 to 5 percent of peptone; here again, myxamoebae were few in number and scattered; however, a few micropseudoplasmodia developed, and from these minute sorocarps were formed.

A third experiment was performed in order to determine whether the myxamoebae could feed upon products which were of bacterial origin but which were not contained within the bacterial cells. Large colonies of *Escherichia coli* were grown upon a favorable medium and when 3 days old were scraped off and suspended in approximately 10 volumes of water. This suspension was vigorously shaken and was then filtered through an L2 Chamberland filter. The unheated sterile filtrate was solidified with sterile agar, and Petri plates of this medium were subsequently inoculated with pure spores of *Dictyostelium discoideum*. Spore germination occurred, but no vegetative growth of the slime mold took place. Thus it was indicated that soluble products resulting from bacterial growth could not be used as nutriment by the myxamoebae of *D. discoideum*.

The writer's results obtained with peptone-rich agar are especially interesting, since Nadson (*12*) reported a meager growth of *Dictyostelium mucoroides* in the absence of bacteria in a solution containing phosphates and 5 percent of peptone. The correctness of Nadson's work was later questioned by Potts (*17*) and Pinoy (*16*), on the basis of their studies with that slime mold.

The studies reported by Nadson (*12*) on *Dictyostelium mucoroides* and the writer's studies on *D. discoideum* would indicate that through continued study some synthetic medium will probably be found upon which a fair growth and normal development of the Dictyosteliaceae can take place in the complete absence of bacteria.

RELATION BETWEEN DICTYOSTELIUM DISCOIDEUM AND ASSOCIATED BACTERIA

A role of importance was first attributed to the accompanying bacteria by Nadson (*12*), who, working with *Dictyostelium mucoroides* in association with *Bacillus fluorescens liquefaciens*, reported that the slime mold and associated bacteria were symbionts. He believed that the bacteria favored the *Dictyostelium* by creating an alkaline reaction in the culture, while the *Dictyostelium* favored the bacteria by supplying them with foodstuffs in the form of mucus, empty spore cases, etc. Skupienski (*21*) likewise considered *D. mucoroides* to be symbiotic with the associated bacteria. He based his belief upon the following points: (1) *D. mucoroides* was always associated with bacteria and the habitual associate was a single species, *B. fluorescens liquefaciens* (*12, 15, 20*); (2) bacteria were often seen clustered at the posterior end of the myxamoebae in the region of the contractile vacuole, and this he interpreted as indicating that the myxamoebae excreted something that favored the bacteria.

Potts (*17*) observed that *Dictyostelium mucoroides* grew only in the presence of bacteria and that it consumed the bacterial colonies in which it fed. He found no evidence to indicate that the bacteria

gained anything from the association, and concluded that since the slime mold could grow with at least four different species the relationship could not be one of symbiosis.

In terming *Dictyostelium mucoroides* a "bacteriophage", Vuillemin (*24*) obviously considered the relationship as one approaching parasitism of the bacteria by the slime mold. Going one step further, Pinoy (*16*) reported that the Dictyosteliaceae studied by him could grow only in the presence of living bacteria and considered that the myxamoebae were truly parasitic upon the bacterial colonies in which they grew.

If Ward's (*25*) definition, that symbiosis is the cooperation of two associated organisms to their mutual advantage, is accepted, the writer's investigations gave no indication of a true symbiosis between *Dictyostelium discoideum* and any of the bacteria that have at different times accompanied it. As has been shown, the myxamoebae of this species ingested and digested the associated bacteria, and the colonies of bacteria were in the majority of cases completely consumed. On the other hand, there was no evidence that the growth of the accompanying bacteria was enhanced in any way by the presence of the slime mold. Further, the fact that *D. discoideum* grew equally well with many species of bacteria points to an absence of symbiosis. If any degree of symbiosis had existed between the slime mold and the accompanying bacteria, the following conditions should have prevailed: (1) *D. discoideum* should have grown better in association with *Vibrio alkaligines*, the bacterium that accompanied the original culture, than in association with bacteria isolated from other species of *Dictyostelium;* (2) *D. discoideum* should have grown better in association with bacteria isolated from other species of *Dictyostelium* than in association with bacteria isolated from species of the related genus *Polysphondylium;* and (3) *D. discoideum* should have grown better in association with bacteria isolated from species of the Dictyosteliaceae in general than in association with the bacteria that, so far as known, had never been associated with these slime molds. As clearly shown by the experiments discussed above, such results were not obtained (tables 1 and 2).

On evidence from his own studies, the writer is led to consider the relationship between the two organisms as one of a modified or specialized type of parasitism of bacteria by the myxamoebae. The term "modified parasitism" is used because one does not usually think of an organism being parasitized by another organism of greater size that itself. On the other hand, if one considers a bacterial colony as a distinct entity in itself rather than as an assemblage of individuals (i. e., bacterial cells), then Pinoy's view that the myxamoebae are parasitic upon colonies of bacteria is thoroughly accurate. Perhaps more correctly the myxamoebae should be regarded as predatory on the bacteria.

It is often convenient to refer to the associated bacteria as "host" to the *Dictyostelium*, and to the different bacteria with which *D. discoideum* will grow as its "host range." It should, however, be remembered that these terms are not used here in the usual sense, for, as in the case of parasitism, one does not usually think of an organism being host to a much larger organism than itself.

DISCUSSION

Because of certain unique features in its developmental history, *Dictyostelium discoideum* is a peculiarly favorable species with which to study problems pertaining to the relation between a member of the Dictyosteliaceae and the bacteria that accompany it. The vegetative stage in this and other species of the genus is indistinguishable; and similarly, the formation of pseudoplasmodia in *D. discoideum* is like that in other Dictyostelia. After the formation of the pseudoplasmodia, however, marked differences in behavior occur. The compact pseudoplasmodium of *D. discoideum* typically leaves the bacterial colony in which it develops, migrates for a greater of less distance across the agar surface, and then builds an erect sorocarp. On the other hand, the pseudoplasmodia of other species of the Dictyosteliaceae do not migrate, but build their sorocarps directly from the points of origin of the pseudoplasmodia within the bacterial colony. From the standpoint of cultural studies this difference is of the greatest importance. In migrating across the agar surface, the pseudoplasmodium of *D. discoideum* divests itself of bacteria and subsequently forms an isolated sorocarp upon the sterile agar surface. Such sorocarps regularly bear spores that are free from bacteria. In other species, where the base of the stalk always remains within the bacterial colony, bacteria are carried up the sorocarp during its formation or ascend the sorocarp shortly after its development is complete, and the spores borne by it are not regularly free from bacteria.

Dictyostelium discoideum can at will be placed in pure-mixed culture with any pure culture of bacteria simply by inoculating spores from isolated sorocarps into colonies of the selected bacteria. The ease of this operation stands in sharp contrast with the methods employed by Potts (*17*) and Pinoy (*16*) for securing pure-mixed cultures of *D. mucoroides* in association with bacteria other than those with which they isolated the slime mold. Potts (*17*) initially isolated *D. mucoroides* in association with *Bacterium fimbriatum*. To secure a culture of the slime mold in association with *Bacillus megatherium* alone, he cultured *Dictyostelium* in successive colonies of *B. megatherium* until *Bact. fimbriatum* was wholly eliminated. The technique employed by Pinoy (*16*) was likewise tedious. *D. mucoroides* was grown in pure-mixed culture with *B. fluorescens liquefaciens*, and spores from such cultures were suspended in water and drawn into capillary tubes, which were subsequently exposed to a temperature of 56° C. for 2 minutes. This exposure, according to Pinoy's report, killed the bacteria, while the majority of the spores of *D. mucoroides* remained viable. Conversely, Skupienski (*20*) reports that he attempted to free spores of the same slime mold from *B. fluorescens liquefaciens* by this method and found that the bacteria were more heat-resistant than the *Dictyostelium* spores.

The present studies show that a member of the Dictyosteliaceae can grow in association with a much greater number and with a wider range of bacterial species than was known from previously published works. Nadson (*12*), Vuillemin (*24*), and Skupienski (*20*, *21*) cultivated *Dictyostelium mucoroides* in association only with the fluorescent bacteria with which they isolated the slime mold. Potts (*17*) succeeded in growing the same slime mold in association with three species of bacteria other than *Bacterium fimbriatum*, which originally

accompanied his culture of *Dictyostelium*. Pinoy (*15*, *16*) isolated *D. mucoroides* with *Bacillus fluorescens liquefaciens* and subsequently cultivated it in pure-mixed culture with seven additional species of bacteria. With the single exception of *Rhizobium leguminosarum*, the writer succeeded in growing *D. discoideum* in association with each of the 42 pure cultures, representing 32 species of bacteria, which were investigated in this survey. Included among this number were a large number of common saprophytic forms and several bacteria that had been isolated from cultures of Dictyosteliaceae. From the standpoint of classification and natural groupings, the species studied included members of the following families (after Bergey et al. (*1*)): Bacteriaceae, Bacillaceae, Coccaceae, Spirillaceae, and Nitrobacteriaceae (tables 1 and 2).

Particular attention was given in the present study to establishing standardized culture practices and methods that would enable one to study and compare quantitatively the growth of a species of the Dictyosteliaceae in association with different bacteria. Objections may possibly be raised to the methods employed. However, after extended study of the problem, the writer is convinced that so long as the culture medium is kept uniform in composition and in the amount used per plate and so long as the number of colonies and the disposition of these colonies on the culture plate are kept constant, the number (and size) of sorocarps produced per bacterial colony affords the most reliable and the most convenient measure of the growth of a species of the Dictyosteliaceae.

Appreciable variation in the amount of growth of *Dictyostelium discoideum* occurred in association with the different bacterial species, and even with different strains of the same species (figs. 2 and 3). This variation in growth of the slime mold could be attributed either to the amount of bacterial growth or to the availability of the bacteria. In the majority of cases, the bacterial colonies were wholly consumed and the amount of *Dictyostelium* growth was directly proportional to the amount of bacterial growth. In other cases, the conditions within the bacterial colonies were not entirely favorable to *Dictyostelium* and factors other than the quantity of bacteria governed the amount of growth of *D. discoideum*.

When grown upon hay-infusion agar, Gram-negative and Gram-positive bacteria alike afforded favorable nutriment for *Dictyostelium discoideum*. Thus the writer's investigations corroborate, in this regard, the results obtained earlier by Potts (*17*), who reported that *D. mucoroides* grew well with either Gram-negative (*Bacillus fluorescens liquefaciens* and *Bacterium fimbriatum*) or Gram-positive (*Bacillus subtilis* and *B. megatherium*) bacteria. Contrary to these results, Pinoy (*16*) reported that *D. mucoroides* could not grow with Gram-positive bacteria (*B. subtilis* and *B. megatherium*), and attributed Potts' (*17*) earlier success to impure cultures in which small Gram-negative bacteria accompanied unnoticed the larger Gram-positive bacilli. Vuillemin (*24*) and Pinoy (*16*) attempted unsuccessfully to grow *D. mucoroides* in pure-mixed culture with *B. pyocyaneus*, whereas the writer succeeded in cultivating *D. discoideum* in association with this bacterial species.

What, then, is the explanation of this lack of agreement among students of the Dictyosteliaceae? Can the disparity in results be explained by an essential difference between *Dictyostelium mucoroides*

and *D. discoideum* in their ability to feed upon certain bacteria? The writer's studies do not indicate such an explanation, for in his experience the growth of *D. mucoroides* and *D. discoideum* in association with the same bacterial species upon the same medium was comparable both in amount and in vigor. Furthermore, Potts and Pinoy obtained results which were diametrically opposed even when they studied the same species of slime mold (*D. mucoroides*) in association with the same species of bacteria (*Bacillus subtilis* and *B. megatherium*). The writer believes that the primary explanation of the difference in results obtained by students of this group consists neither in a difference between the species or strains of *Dictyostelium* studied nor in a difference between the strains of bacteria investigated, but in the difference between the media employed as substrata for the bacteria. Potts (*17*) used maize-extract media and noted that its chief advantage resided in the fact that its nutrients were relatively unavailable to the bacteria tested. The nutritive composition of the hay-infusion agar employed by the writer is not known, but it was not a rich medium and the nutritive materials it contained were not of a type that would be readily available to the bacteria studied. Upon the basis of the writer's studies with *D. discoideum* the following conclusion can be stated as a general rule The more dilute a medium is in nutrients, or the less accessible its nutrients are to a large number of different bacterial species, the more probable it is that a member of the Dictyosteliaceae will be able to grow in association with a large number of bacterial species upon that medium.

It is on this basis that the writer believes the difference in results obtained by students of the Dictyosteliaceae are to be explained. To understand the whole situation, the composition and the concentration of the media and the fermentive ability of the associated bacteria must be known. This matter is now being investigated.

Contrary to the views of Nadson (*12*) and Skupienski (*21*), who worked with *Dictyostelium mucoroides*, the writer found no indication of a symbiotic relationship between *D. discoideum* and the bacteria with which it was associated. Rather, the myxamoebae of the slime mold should be considered as predatory upon the accompanying bacteria. This view, in general, conforms to those earlier set forth by Potts (*17*), Vuillemin (*24*), and Pinoy (*16*). There was no indication that *D. discoideum* could grow better in association with bacteria which had been isolated from cultures of Dictyosteliaceae than in association with common saprophytic bacteria which, so far as known, had never been associated with slime molds. Furthermore, there was no indication that the Dictyosteliaceae are habitually associated in nature with the fluorescent bacteria as indicated by the investigations of earlier workers (*12*, *15*, *20*, *24*). The evidence would indicate that it is purely a matter of chance what soil bacteria the slime mold happens to be growing with at the time isolation is made. It is not considered significant that the majority of the writer's cultures of the Dictyosteliaceae were associated with single species of bacteria (table 2), for other species of bacteria, which probably accompanied the slime molds at the time of their original isolation, could have been weeded out by the repeated transfers incident to laboratory cultivation.

Finally, the question arises concerning the possible significance of the fact that *Dictyostelium discoideum* is able to grow in association

with a large number of bacterial species belonging to widely separated groups. *D. discoideum* is not widely distributed in nature and it is probable that this slime mold is not an active constituent of the soil flora. On the other hand, from the work of Raper and Thom (*19*) it is known that other species of this group are common in soil and in decaying vegetation, and it is possible that these may play a more important role in soil economy than has hitherto been attributed to them. Assuming that such common forms as *D. mucoroides* and *Polysphondylium violaceum* can likewise feed upon an equally wide variety of different bacteria, it is entirely possible that under certain circumstances they may alter the bacteriological population of the soil appreciably.

Another significant point brought out by these studies consists in the fact that *Dictyostelium discoideum* is shown to be an exceptionally favorable organism with which to study experimentally the relation and interaction between a small amoeba (i. e., myxamoeba) of the soil and the bacteria upon which it feeds. The following characters recommend it for such experimental studies: (1) It is easily cultivated in the laboratory; (2) it will feed upon a wide range of bacteria belonging to diverse groups when these are grown upon favorable media; (3) it can be placed in pure-mixed culture with any bacterial species at will by selecting isolated sorocarps as spore sources; and (4) it forms characteristic fruit structures which immediately identify the species.

SUMMARY

Dictyostelium discoideum regularly grows within the limits of bacterial colonies, but the pseudoplasmodia typically leave the bacterial colonies in which they develop and migrate for a greater or less distance across the agar surface before forming sorocarps.

During their migration, the pseudoplasmodia divest themselves of all bacteria, and the spores borne in sorocarps formed at a distance of 0.5 cm or more beyond the limits of the bacterial colony are regularly free from bacteria.

The type culture of *D. discoideum* was accompanied by the single bacterial species *Vibrio alkaligines* Lehm. and Neum. However, by selecting isolated sorocarps, which are bacteria-free, as spore sources, the slime mold could be readily grown in pure-mixed culture with other bacteria.

Standardized culture practices were employed and methods were developed whereby the growth of *D. discoideum* in association with different bacteria could be quantitatively compared. The amount of growth was ascertained by determining the average number of large, medium, and small sorocarps per colony. Quantitative comparisons of the growth with different bacterial associates were made by converting the sorocarps of all sizes into terms of medium sorocarps. For such a unit the term "medium-sorocarp equivalent" has been used.

D. discoideum was grown in association with a large number of saprophytic bacteria, including representatives of such diverse groups as the Gram-negative, nonspore-forming Bacteriaceae, the Gram-positive, spore-forming Bacillaceae, the Coccaceae, the Nitrobacteriaceae, and the Spirillaceae.

In the majority of cases, the bacterial colonies were completely consumed by the feeding myxamoebae, and the amount of growth of *D. discoideum* was directly proportional to the growth of the bacteria. In other cases, the amount of growth was governed by the physical character of the bacterial colonies or by unknown factors.

D. discoideum grew well in association with either Gram-negative or Gram-positive bacteria. On the whole, somewhat better growth occurred with Gram-negative than with Gram-positive species. However, there were exceptions to this rule, for very poor growth of the slime mold occurred with some Gram-negative species, whereas very good growth occurred with some Gram-positive forms.

The growth and development of *D. discoideum* in association with bacteria isolated from other members of the Dictyosteliaceae closely resembled that with common saprophytic bacteria. There was no indication that the Dictyosteliaceae were regularly associated in nature with any particular species or group of bacteria.

The sorocarps were essentially alike in all cultures studied except those with *Serratia marcescens*, where the sorocarps were of normal form but were red in color owing to the presence of a bacterial pigment, and those with *Micrococcus* sp., where the sorocarps were of normal color but were characterized by closely spiral sorophores.

The myxamoebae of *D. discoideum* feed by the ingestion and digestion of bacterial cells. Spores of the Gram-positive bacilli are ingested but are not digested.

The myxamoebae of *D. discoideum* can feed upon bacterial cells that have been killed by heat or by exposure to ultraviolet light; a less luxuriant but normal growth and development of the slime mold occurs in such cultures.

A very meager and abnormal vegetative growth of *D. discoideum* was obtained upon pea-broth agar and upon peptone-rich agar, in the total absence of bacteria.

The myxamoebae of *D. discoideum* are predatory upon the accompanying bacteria and there is no indication that the bacteria gain anything from their association with the slime mold. Therefore, the relationship between the two organisms cannot be regarded as one of symbiosis.

D. discoideum affords a particularly favorable organism with which to study problems pertaining to the relation between a small amoeba of the soil and the bacteria upon which it feeds.

Species of the Dictyosteliaceae may be capable of appreciably altering the bacteriological flora of decaying vegetation in soils.

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